DISSERTATION

CLIMATE EXTREMES IN GRASSLANDS: WHAT'S NEXT?

Submitted by

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ABSTRACT

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As a consequence of warming temperatures under climate change, precipitation extremes like drought, wet years, and deluges (large rainfall events) are increasing. Increasing hydrological extremes have been observed across many ecosystem types, but grassland ecosystems may be particularly vulnerable as they are typically water-limited and highly sensitive to changes in precipitation amount and patterns. Prior research demonstrates the strong relationships between precipitation and grassland structure and functioning, but numerous studies have also identified high variability in grassland responses to that same amount in precipitation in different years. Legacy effects, or the effects of climate extremes that persist after an extreme subsides, are one explanation for variability in responses. Alterations in resources or ecosystem structure may begin during a climate extreme and persist after the extreme ends as legacies. Legacy effects in grasslands may be positive, negative, or a combination of both. Most of our understanding of legacy effects comes from observational and experimental studies that evaluate responses following the end of some extreme period. However, increases in “hydroclimate whiplash” – or rapid transitions between dry and wet extremes – and consecutive drought or wet years are expected under future climate change. Thus, it is increasingly important to study the interactive effects of past and current extremes.

In this dissertation, I use data collected from both field experiments with precipitation manipulations and during natural extreme years to compare grassland responses to extremes and legacy effects following extremes. Each chapter of my dissertation presents results at least in part from the semiarid shortgrass steppe in northern Colorado, USA – spanning over a decade of data altogether – to compare legacy effects at multiple temporal scales and from several types of precipitation extremes. My research overall demonstrates the high sensitivity of grasslands to changes in environmental conditions, especially in the shortgrass steppe, and provides examples of both positive (greater responses than expected) and negative (lower than expected) legacy effects following extremes. The results of my dissertation contribute to our understanding of legacy effects and interactions of past and future extremes. These results can be used to make better-informed management decisions in grasslands threatened by climate extremes, and should be built on in the future with further study of the mechanisms of legacy effects of extremes.

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CHAPTER 1: INTRODUCTION

Human influence, including fossil fuel and aerosol emissions and land-use change, has contributed significantly to rapid increases in global mean surface temperatures since pre-industrial times (Gulev et al. 2021). Greenhouse gas forcing is the dominant driver of rising temperatures and increases in hot extremes (Seneviratne et al. 2021), and the water holding capacity of the atmosphere increases by 6–7% per 1 ºC of warming, leading to greater precipitation inputs during wet seasons or events (Douville et al. 2021; Hegerl et al. 2015). At the same time, warming can increase evaporative demand and increase the severity or frequency of droughts at a regional scale (Douville et al. 2021; Seneviratne et al. 2021). These consequences of warming temperatures are not mutually exclusive – areas can be projected to see both increased precipitation amounts as well as increases in drought or aridity, often attributed to shifts in seasonal dynamics (e.g., wetter springs and drier summers; Hajek and Knapp 2022; Knapp et al. 2020), consecutive opposing extreme years (Swain et al. 2018; He and Sheffield 2020; Zhang et al. 2021), or shifts towards aridity despite increased precipitation in areas where increased potential evapotranspiration dominates (Seager et al. 2018). Extreme precipitation events and seasons can have important consequences – both ecological and societal – such as changes to the amount, timing, or quality of forage for domestic and native grazers (Craine et al. 2010; Boone et al. 2018), or food and water scarcity during drought (Raza et al. 2019; Liu et al. 2022). Observations of increasing hydrological extremes exists across ecosystem types (Huntington 2006; Zeppel et al. 2014; Knapp et al. 2015; Du et al. 2020; Tabari 2020; Chiang et al. 2021; Zhang et al. 2021). Thus, this remains an important topic for current and future research.

Grassland ecosystems are estimated to cover ~ 40% of Earth's terrestrial surface and are particularly sensitive to changes in precipitation amounts and patterns, making them especially vulnerable ecosystems under future climate change (O'Mara 2012; Noy-Meir 1973; Sala et al. 1992; Stuart-Haëntjens et al. 2018; Hoover et al. 2021). The impacts of changing precipitation regimes on grassland net primary productivity (NPP) have been studied extensively, but there remains considerable uncertainty in estimated effects on NPP (Kröel-Duley et al. 2022; Smith et al. 2024). Aboveground NPP (ANPP) has been an area of research focus especially because there is an overall strong positive relationship between ANPP and precipitation (ANPP–PPT; Huxman et al. 2004; Maurer et al. 2020; Felton et al. 2021). ANPP contributes to multiple important grassland ecosystem services – primarily as forage for domestic and native grazers and as a means for carbon storage and further sequestration (Milchunas et al. 1988; O'Mara 2012; Poulter et al. 2014; Ahlström et al. 2015; Bengtsson et al. 2019).

Numerous studies have now assessed productivity responses to drought, deluges (extreme large rain events) and wet years (Knapp et al. 2024; Post and Knapp 2020, 2021; Petrie et al. 2018; Chen et al. 2025), and asymmetries in responses to these contrasting extremes (Wilcox et al. 2017; Dai et al. 2025). However, most climate extremes occur as part of "compound events" – or interacting events that occur in similar regions or close in time (Zscheischler et al. 2018). For example, the same region may see a heat wave during a drought or sequences of multiple extreme precipitation years. Previous theory and experiments have suggested repeated similar extremes would have effects greater in magnitude than a single occurrence (Oesterheld et al. 2001; Sala et al. 2012; Petrie et al. 2018; Peters and Savoy 2023), but the effects of opposite extremes, such as deluge during drought, are less clear (Sala et al. 2012; Hoover et al. 2022). With growing evidence of fluctuations between extreme high and low precipitation years (Swain et al. 2018; He and Sheffield 2020; Zhang et al. 2021), further study of compound and contrasting extremes should be prioritized.

Prior studies of precipitation extremes in grasslands demonstrate strong ANPP–PPT relationships. However, ANPP can vary > 2-fold with the same annual precipitation during different years (Lauenroth and Sala 1992, Briggs and Knapp 1995; Nippert et al. 2006; Fahey and Knapp 2007; Felton et al. 2019). Estimates of ANPP during a given year are often limited when only the current conditions are considered but can improve when previous conditions (precipitation or productivity) are also included (Oesterheld et al. 2001; Sala et al. 2012; Dudney et al. 2017; Petrie et al. 2018; Hahn et al. 2021; Vincente-Serrano et al. 2022; Peters and Savoy 2023; Chen et al. 2025; Goodman and Felton 2025). Legacy effects – the effects of drought or extreme wet periods that persist after the anomaly has ended (Sala et al. 2012) – are one possible explanation for such variability in ANPP estimates.

There have been several long-term studies to determine the implications of legacy effects from previous-year precipitation (Lauenroth & Sala 1992; Sala et al. 2012; Petrie et al. 2018; Hoover et al. 2021; Peters and Savoy 2023) and production (Oesterheld et al. 2001; Hoover et al. 2021; Goodman and Felton 2025). Several short-term studies have also identified legacy effects of previous drought (Griffin-Nolan et al. 2018) or late-season deluge additions (Hajek and Knapp 2024). Legacies, or the alterations in resources or ecosystem structure that drive legacy effects, have been identified as increased or decreased soil water (Monger et al. 2015; Liu et al. 2025), changes in nutrient availability (Birch 1958; Evans and Burke 2013), drought-induced mortality of specific species or functional groups (Sun et al. 2022; Dudney et al. 2017) and many other biotic or abiotic changes. Legacy effects in grasslands can be mostly positive (having a greater response than expected based on current-year conditions; Griffin-Nolan et al. 2018; Hahn et al. 2021; Goodman and Felton 2025), negative (lower responses than expected; Griffin-Nolan et al. 2018; Liu et al. 2025), or a combination of both (Sala et al. 2012; Gong et al. 2020; Peters and Savoy 2023).

Much of our current knowledge of grassland responses to precipitation extremes comes from manipulative and observational studies that focus on a single type of disturbance (e.g. single seasons or years, a series of multi-year drought; Zscheischler et al. 2018), so, naturally, our understanding of legacy effects similarly is based on mostly studies of isolated disturbances. However, because compound climate extremes and "hydroclimate whiplash" (rapid wet-dry transitions; Swain et al. 2025) are expected to continue to increase with climate change, we must consider the interactions of legacies that carryover from previous extremes during current extremes. In my dissertation, I have sought to further our understanding of the interactive effects of past and future extremes in grassland ecosystems.

In the following chapters, I describe three field experiments that involve precipitation manipulations to simulate drought, deluges, and extreme wet seasons which I use to identify and quantify differences in grassland responses to and legacy effects or recovery from precipitation extremes. In Chapter 2, I analyze a decade of drought data from four grasslands across the US Great Plains and (1) compare responses of these grasslands to a one-year natural drought and 4-year experimental drought and (2) compare drought responses and recovery dynamics in different grassland types. I expected to see the greatest reductions in grassland productivity after 4-year experimental drought and delayed recovery (Oesterheld et al. 2001; Sala et al. 2012; Hoover et al. 2014), but little difference between the one-year natural and four-year simulated droughts (Huxman et al. 2004; Sala et al. 2012; Knapp et al. 2015). Chapter 3 and 4 describe results from field experiments that took place at the Central Plains Experimental Range in northern Colorado’s native shortgrass steppe. In the first of these two field projects, I compared the responses to a mid-summer deluge addition after manipulating early spring precipitation. Spring precipitation has been shown as an important determinant of ANPP (Parton et al. 2012; Hoover et al. 2021; Hartman et al. 2020) and this grassland is very sensitivity to deluge additions (Post and Knapp 2020, 2021; Post et al. 2021), so we expected a negative effect of early spring precipitation reduction, but a compensation for this early drying with the later deluge addition. Finally, I conducted a 3-year study involving both precipitation additions and natural extreme drought ambient conditions, scenarios of “hydroclimate whiplash”, with the goal to identify potential buffering or amplifying effects.

The combination of projects presented herein allows for a deeper understanding of legacy effects of climate extremes and the interactions of legacies with continued extremes. Additionally, the multiple comparisons of responses in the shortgrass steppe allow for a novel comparison of legacies at multiple timescales (a single year manipulation, a 3-year study of opportunistic and manipulated extremes, and a 10-year analysis comparing long-term experimental and short-term natural drought), which in this especially sensitive grassland will allow us to further our knowledge of impacts of future climate change.

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CHAPTER 2: EXPERIMENTAL DROUGHT CONSISTENTLY UNDERESTIMATES PRODUCTIVITY RESPONSES TO NATURAL DROUGHT IN FOUR CENTRAL US GRASSLANDS[1]

2.1 Summary

Climate change is increasing the frequency and severity of droughts globally, and grasslands are particularly vulnerable to such hydrological extremes. Drought effects at the ecosystem scale have been assessed both experimentally and through the study of naturally occurring drought, with emerging evidence that the magnitude of drought effects may vary depending on the approach used. We took advantage of a decadal study of four grasslands to directly contrast responses of aboveground net primary productivity (ANPP) to simulated vs. natural drought. The grasslands spanned a ~threefold mean annual precipitation gradient (335–857 mm) and were all subjected to a natural 1-year drought (~40% reduction in precipitation from the long-term mean) and a 4 year experimental drought (~50% precipitation reduction). We expected that the 4 year drought would reduce ANPP more, and that post-drought recovery would be delayed, compared to the 1-year drought. We found instead that the short-term natural drought reduced ANPP more strongly than the simulated drought in all grasslands (~10 to ~50%) likely due to the co-occurrence of higher temperatures and vapor pressure deficits with reduced precipitation. Post-drought recovery was site specific and each site differed in their recovery from the natural and experimental droughts. These results align with past analyses that experiments that only manipulate soil moisture likely underestimate the magnitude of natural

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[1] Condon KV, Carroll CJW, Griffin-Nolan RJ, Slette IJ, Wilkins KD, Smith MD, Knapp AK. 2025. Experimental drought consistently underestimates productivity responses to natural drought in four Central US grasslands. *Oecologia*. 207, 104.

drought events. However, experiments can provide valuable insight into the relative sensitivity of ecosystems to reduced precipitation and soil moisture, a key aspect of drought.

2.2 Introduction

As forecasts for more frequent and severe droughts become reality, quantifying the impacts of drought on ecosystems, including patterns of relative drought sensitivity among ecosystems, has become increasingly urgent (Trenberth et al. 2003, 2014; Ault 2020; Chiang et al. 2021; Vicente-Serrano et al. 2022). Ecosystem drought, defined as an abnormal period of low water availability of sufficient duration to potentially alter ecosystem structure and function (Knapp et al. 2024), has been studied in many ways. Approaches include on-the-ground and remote sensing assessments of naturally occurring droughts across a wide range of ecosystem types (e.g., Wolf et al. 2016; Slette et al. 2019; Lu et al. 2021; Hammond et al. 2022) as well as hundreds of smaller-scale manipulative experiments conducted mostly in short-statured grasslands and shrublands (Beier et al. 2012; Knapp et al. 2024; Smith et al. 2024). Although it has long been recognized that different approaches to studying ecological phenomena can lead to variable outcomes (e.g., Sutherland 2006; Fraser et al. 2013), such variation in the assessment of precipitation anomalies has led to persistent concerns about uncertainty in estimates of drought impacts on terrestrial net primary productivity (NPP; e.g., Kröel-Dulay et al. 2022; Smith et al. 2024). Thus, a research priority for ecologists is to increase our understanding of how drought (natural vs. simulated experimentally) impacts NPP, especially aboveground NPP (ANPP), which provides many essential ecosystem services (food, fuel, and fiber) and plays a central role in the global carbon cycle (Zheng et al. 2003; Fahey and Knapp 2007; Knapp et al. 2014; Ahlström et al. 2015). Small-scale field experiments that reduce precipitation inputs to simulate drought are numerous, but also frequently criticized for a range of shortcomings (Sandel and

Smith 2009; Leuzinger et al. 2011; Beier et al. 2012; Hoover et al. 2018; Yang et al. 2022; Kröel-Dulay et al. 2022). Chief among these are that, while the most common infrastructure used to simulate drought (precipitation reduction shelters, Yahdjian and Sala 2006) is effective at lowering soil moisture, this infrastructure has minimal impacts on air temperature, vapor pressure deficit (VPD), and solar radiation (Gherardi and Sala 2013; Alba et al. 2017; Loik et al. 2019) – all of which are important environmental alterations that co-occur during natural drought periods (De Boeck and Verbeeck 2011; Novick et al. 2016; Kröel-Dulay et al. 2022; Wright and Collins 2024). Indeed, high temperatures and VPD can negatively impact plant growth independent of soil water deficits (Grossiord et al. 2020; Schönbeck et al. 2022; Novick et al. 2024) and when combined with extreme reductions in precipitation, "hot droughts" may lead to catastrophic losses in ecosystem productivity (e.g., Breshears et al. 2005; Dannenberg et al. 2022). While experimental approaches offer many advantages and much can be learned from imposing soil moisture deficits to study drought impacts (Knapp et al. 2024), direct comparisons of how ANPP responds to natural vs. experimental (i.e., simulated) droughts are rare. Such comparisons are needed, however, to provide insight into what can and cannot be inferred from these different approaches (e.g., Sandel et al. 2010; Knapp et al. 2018). Here we conduct such a comparison by taking advantage of a 10-year study (from 2012 to 2021) of four Central US grasslands that span a ~threefold precipitation gradient. During this period, each of these sites experienced a naturally occurring 1-year extreme drought (~40% reduction in precipitation due to a pan-continental drought; Cook et al. 2014; Knapp et al. 2015). Later, all sites were subjected to a simulated 4-year drought (66% reduction in growing season precipitation imposed as part of the Extreme Drought in Grasslands Experiment (EDGE), Carroll et al. 2021). Post-drought recovery was also monitored in each grassland. Because the same experimental plots were sampled throughout the entire 10-year period, including control plots, we can now directly compare the impact of these two droughts as well as recovery from them with consistent site-specific ANPP context (mean and interannual variability). Such context was previously unavailable in past assessments of these grassland responses to drought, so long term averages from areas within the same larger research sites were used as comparisons (Knapp et al. 2015; Griffin-Nolan et al. 2018a, b; Carroll et al. 2021). As a result we can now revise past estimates of drought sensitivity by using the data collected from the same exact plots over 10 years rather than data collected from various locations and potentially with different methods of ANPP estimation within the larger sites. Our goals were to: 1) compare the magnitude of ANPP responses to natural vs. experimental drought in each of four grassland types (a C_4 shortgrass prairie, a C_3/C_4 mixed-grass prairie, a C_4 mixed-grass prairie and a C_4 tallgrass prairie), 2) determine if the relative sensitivity to drought among grasslands varied by drought type, and 3) assess post-drought recovery of ecosystem functioning across these grasslands. We predicted that four years of extreme growing season precipitation reductions (the experimental drought) would impact ANPP more than a 1-year natural drought, and that post-drought recovery in ANPP would be delayed with longer-duration precipitation reductions (Oesterheld et al. 2001; Sala et al. 2012; Hoover et al. 2014). However, we expected that the relative sensitivity to drought (i.e., productivity reduction per unit reduction in precipitation) among these grasslands would not differ between the one-year natural and four-year simulated droughts imposed (Huxman et al. 2004; Sala et al. 2012; Knapp et al. 2015). In other words, although the magnitude of drought impacts on these grasslands might vary by drought type and duration, the relative responses among the grasslands would be consistent.

2.3 Methods

2.3.1 Site Descriptions

The four Central United States grasslands studied represent the major perennial grassland types in the Great Plains. Mean annual precipitation (MAP) at the sites increased from west to east by ~500 mm, with ANPP increasing similarly from ~100 g m^{-2} to nearly 500 g m^{-2} (Fig. 2.1). Interannual variability in precipitation is generally strongly correlated with ANPP both within and across these grasslands, typical of broader patterns across the Great Plains (Fig. 2.1, Sala et al. 1988). Indeed, the slope of the relationship between MAP and ANPP across four sites during our study years (Fig. 2.1) was identical to that previously reported in Sala et al. (1988). The northern mixed grass prairie (HPG) at the High Plains Grassland Research Center in Cheyenne, Wyoming is codominated by the C_3 *Pascopyrum smithii* mixed with C_4 *Bouteloua gracilis*, with the latter species being the dominant grass at the northern shortgrass steppe (SGS) in the Central Plains Experimental Range near Nunn, Colorado. The warmer, more productive grasslands near Hays, Kansas and Manhattan, Kansas included a southern mixed grass prairie (HYS; at the Hays Agricultural Research Center) and an annually burned tallgrass prairie (KNZ; at the Konza Prairie Biological Station), both C_4-dominated. Dominant species of the southern mixed grass prairie (HYS) include *Bouteloua curtipendula*, *Schizachyrium scoparium*, and *P. smithii* and dominant tallgrass (KNZ) species were *Andropogon gerardii* and *Sorghastrum nutans*. The two mixed grass prairie sites were lightly grazed in the two years prior to our study (2010–2011) while the tallgrass and shortgrass steppe study plots had not been grazed by domestic herbivores for >10 years prior to the start of this study in 2012. No sites were grazed over the course of the experiment (2012–2021).

2.3.2 Contrasting the natural vs. experimental drought

In 2012, much of the United States experienced severe drought conditions including all four of the grassland sites included in this analysis (Cook et al. 2014). This pan-continental drought was a relatively rare event in both its extent and severity, but greenhouse gas forcing is expected to increase the occurrence of such droughts in the future (Cook et al. 2014). At the four EDGE sites, annual precipitation was reduced by nearly 40% in 2012 which in turn reduced ANPP at each site by 25–50% compared to long-term averages (LTA) from nearby areas (Knapp et al. 2015). The legacy effects of this drought (Vilonen et al. 2022) continued to affect ANPP at some sites into 2013 (Griffin-Nolan et al. 2018a, b). The EDGE plots were constructed starting in 2012, but the manipulated drought treatments did not start until 2014 at each site and continued through 2017. EDGE was designed as a coordinated distributed experiment (Fraser et al. 2013) with identical methods employed at the four sites. We used data collected from EDGE beginning in 2012 to monitor responses to the natural drought and one year of recovery in 2013. We then compared those responses to the manipulated drought treatments from 2014 to 2017, and similarly monitored recovery from the four year experimental drought through the four years post-drought (2018–2021). EDGE compared two drought treatments, both causing a ~66% reduction in growing season precipitation, but imposed in slightly different ways. The “chronic treatment” reduced all rain events by 66% over the entire growing season and an “intense treatment” eliminated all rain events, but for a shorter portion of the growing season. One replicate of each treatment was randomly assigned into one of three plots in each of the 10 experimental blocks at each site. Thus, each block consisted of three 6 × 6 m plots (n = 30 independent plots per site), two of which were covered with partial or full transparent roofs for all or part of the growing season and one with the shelter structure but no roofs present, to act as an infrastructure control (with ambient precipitation). Each 36 m^2 plot was hydrologically isolated from its surroundings using plastic sheeting buried belowground and aluminum flashing partially buried to prevent aboveground overland water flow. Plastic roofs were installed and removed each year such that treatments were imposed from ~April 1 through mid-September. Previous studies with these types of shelters have found little effect of micrometeorological differences caused by the roofs on plant responses (Loik et al. 2019), with the largest differences in air temperatures happening at night. Photosynthetically active radiation (PAR) can be reduced by shelters, though the implications on plant physiological responses overall are minimal (Yahdjian and Sala 2002; English et al. 2005; Signarbieux and Feller 2012; Loik et al. 2019). Therefore, our climate variables for VPD and temperature (described below) are from outside of roofing structures, but should be comparable to levels under roofs as well. Further details on drought treatments and experimental design can be found in Carrol et al. (2021). After the 4-year experimental drought treatments ended, we monitored post-drought ANPP for an additional four years (2018–2021). Carroll et al. (2021) analyzed the effects of the two types of drought treatments on ANPP during the experimental drought period (2014–2017) and found that, while droughted plots differed significantly from ambient plots, the two drought treatments (chronic vs. intense drought) seldom differed significantly from each other. Thus, we combined them into one experimental drought treatment for this analysis. By combining the drought treatments, we were left with n = 10 ambient plots per site and n = 20 drought plots for site, rather than the original n = 10 of each (ambient, chronic, and intense drought). When directly comparing or combining responses of ambient and droughted plots (such as percent reductions or drought sensitivity – see below), we used the one ambient plot and the average of the two drought plots from the same block.

2.3.3 Climate variables

We compiled climate data from a variety of sources for this analysis. During the experimental drought period (2014–2017), ambient precipitation was measured at each site with tipping-bucket rain gauges. Inputs into the droughted plots were calculated based on estimates of reductions from drought shelter designs and were adjusted as needed using soil moisture data to account for any rainfall blowing into plots, temporary roof damage, etc. During pre-treatment and post-drought recovery periods (2012–2013 and 2018–2021), precipitation inputs were determined from a combination of site rain gauges when available, the nearest weather station at the research sites, or the nearest National Oceanic and Atmospheric Administration (NOAA) stations. To assess long term climate averages, we combined our experimental climate data with earlier NOAA records (1990–2011), using daily precipitation data from the closest NOAA station gap-filled as needed with data from surrounding stations (90% of observations were from stations within 15 km of the sites with the 10% used for gap-filling taken from further NOAA stations; Menne et al. 2012a, b). Temperature and vapor pressure deficit (VPD) data were retrieved using PRISM for all years (1990–2021, PRISM Climate Group 2024). All climate data were collected and analyzed at the site-level, and we defined the growing season as April 1–September 15 for all sites and all variables.

2.3.4 ANPP responses

ANPP was measured at each site at the end of each growing season by harvesting all aboveground biomass within 20 × 50 cm quadrats (typically three per plot, although occasionally these precision replicates were reduced to two or rarely one – 11 and 4% of all plots, respectively – only during the 4-year recovery period). Harvested quadrats were randomly located within subplots dedicated to destructive sampling and flagged to avoid resampling in consecutive years. Biomass was sorted into C3 and C4 grasses, forbs, and woody (if present) biomass, as well as previous years' dead material, before being dried at 60˚C for 48 h and weighed to the nearest 0.01 g. Ten-year ANPP averages were calculated from the control (ambient precipitation) plots at each site from 2012 to 2021 (n = 30 plots per site, except for KNZ where plots were not yet established in 2012, so we used n = 5 plots from a nearby area with similar soils and topography). From 2014 to 2021, we used only the ambient plots (n = 10 plots per site) that had not be exposed to experimental drought treatments in the calculations of ANPP LTA's. In total, this allowed us to estimate ANPP LTA's with > 500 samples collected across all site's ambient plots over all years. As noted above, this provided us with a more precise estimate of ANPP and its interannual dynamics compared to previous analyses, which had to rely on ANPP data from past studies that varied in collection methods, location, and sampling intensity (Knapp et al. 2015). To quantify drought responses, we calculated the proportional (%) reduction in ANPP in droughted vs. ambient plots for each year (2014–2017) of the experimental drought (n = 10 per site – calculated as the average reduction of ANPP in the two drought plots compared to the one ambient plot in each block). Because all plots, including ambient plots, were subject to the natural drought in 2012, we calculated the proportional reduction in ANPP in response to the 2012 drought relative to the mean ambient ANPP for the 9 years after this drought. Similar comparisons were made during the recovery years – in 2018–2021 comparing droughted vs. ambient plots, and in 2013 comparing ANPP at each site to the ambient ANPP average. Because control (ambient) plots were not available for the 2012 drought, we statistically assessed ANPP responses to drought and recovery post-drought separately for the natural and experimental droughts (see below). Further, to better match time scales, we assessed the ANPP response to the experimental drought in two ways: focusing on just the first year of drought (to match the duration of the natural drought) as well as the average ANPP response across the entire 4-year experimental drought period. Recovery periods were similarly assessed (1-year recovery period from the natural drought, and both 1-year and 4-year-averaged recovery from experimental drought). We evaluated time (Year) as a variable in the 4-year drought and recovery periods, and although ANPP did differ significantly among years, there were no clear temporal patterns for either drought duration or post-drought recovery (see Fig. 2.3a below). Thus, we focused on the average 4-year response and recovery at each site. Finally, because previous estimates of relative drought sensitivity were determined by calculating the reduction in ANPP per unit change in precipitation (g m^{-2} mm^{-1}; Huxman et al. 2004; Knapp et al. 2015) we calculated drought sensitivity in a comparable way, as productivity (ANPP) changes divided by precipitation (PPT) changes.

For natural drought:

$$\frac{ANPP_{2012} - ANPP_{2013-2021\ average}}{PPT_{2012} - PPT_{30-yr\ average}}$$

And for experimental drought:

$$\frac{ANPP_{drought\ plot} - ANPP_{ambient\ plot}}{PPT_{drought\ treatments} - PPT_{ambient}}$$

where long-term averages (ANPP 2012–2021) for each site were used as “ambient” values for the natural drought period (2012–2013, when no undroughted plots were available) and the actual observed ambient and drought plot measurements for the experimental drought period (2014–2021). These estimates of sensitivity were also used to compare directly to previous estimates of drought sensitivity according to the Huxman-Smith model (Huxman et al. 2004).

2.3.5 Statistical analysis

All statistical analyses were performed in R version 4.3.2 (R Core Team 2023). We first compared climate variables (precipitation, air temperature, and VPD at the site-scale) between the natural drought year (2012) and averaged across all experimental drought years (2014–2017). Since precipitation varies considerably across years (Fig. 2.2a), we calculated each year's annual precipitation in terms of the percent of the LTA precipitation for each site. We then used the % LTA precipitation in 2012 as the reference value in a one-sample t-test compared to the average % LTA precipitation from the four years of experimental droughts (using only the precipitation from the drought treatment reductions; Fig. 2.2b). We also compared daily air temperatures and VPDs during the natural and experimental drought periods using the average daily temperature or VPD during the growing season. We created simple linear regressions using the lme4 package in R (Bates et al. 2015) and the car package Anova function (Fox and Weisberg 2019) with daily temperature or VPD as the response variable and site and drought type (natural or experimental) as fixed effects, and since their interaction was significant, we used the emmeans package (Lenth 2024) to assess pairwise comparisons for drought type differences within each site (Table A1.5). Measures of ANPP (g m^{-2}) were analyzed at the plot level (n = 20 drought and 10 ambient plots per site) and ANPP sensitivity (g m^{-2} mm^{-1}) at the block level (n = 10 per site because we combined the two drought plots with the one ambient plot in each block, as explained above). Blocks and plots remained consistent throughout the 10-year period, so any analyses of differences in multiple years included plot or block as a random effect to account for repeated measures in the same experimental units over time and additionally included a "time" or "period" effect with plot or block when plots were measured across treatments (e.g., when comparing plots across the natural and experimental drought periods). Before analyzing any ANPP data, we checked for and removed ANPP outliers within groups for each site and each year since substantial variability in annual and site ANPP is expected. We used the interquartile range (IQR) method for identifying outliers and only removed any observations that were defined as extreme (± 3•IQR below the first quartile or above the third) and only if no clear ecological explanation existed for those ANPP fluctuations (such as large forbs driving increased biomass in particular plots). Of the ~1200 plots harvested for ANPP across all sites and years, only 20 (~1.7%) were determined to be outliers and dropped before analysis. Differences in ANPP were assessed using repeated measures mixed effects ANOVAs within each period: the natural drought and recovery (2012 vs. 2013), during the experimental drought (2014–2017), and in the four years of recovery following experimental drought (2018–2021; Table A1.6). Within each of these periods, we fit separate linear regressions using the lmer function of the lme4 package and anova function of the lmerTest package (Bates et al. 2015; Kuznetsova et al. 2017) with ANPP (g m^{-2}) as the response variable. Site, Year, experimental drought treatment, and their interactions were the fixed effects (except in 2012–2013 where only Site and Year were fixed effects as no experimental drought treatments had begun yet) and plot as a random effect to account for repeated measurements in the same plots over time. In 2012, experimental plots at KNZ were not yet set up, so we used estimates of ANPP from a nearby site, though our results do not change whether KNZ is analyzed along with the other sites in 2012 or on its own. For all periods, the interactions between Site, Year, and Treatment (when included) were significant, so we followed ANOVAs with pairwise comparisons again using the emmeans function (Table A1.6; Lenth 2024). Pairwise comparisons of 2014–2018 annual ANPP estimates allowed us to identify significant reductions from the experimental drought treatments compared to ambient precipitation plots, but in 2012–2013, all plots were under the same ambient conditions – so we additionally compared 2012 and 2013 ANPP estimates to the long term average (LTA) ANPP for each site using simple linear regressions with Site and Period (2012 or 2013 alone as one period and the other 9 years as the second period) as fixed effects, and again followed with pairwise emmeans comparisons to check for differences within each Site. We calculated ANPP sensitivity for 2012 and during the 2014–2017 experimental droughts as the reduction in ANPP (g m^{-2}) divided by the reduction in precipitation (mm), with 2012 ANPP and precipitation compared to site LTA's and 2014–2017 ANPP and precipitation in droughted plots compared to ambient plots in the same blocks. We compared ANPP sensitivity during the natural drought to both the first year of the experimental drought (2014) and across all years of the experimental drought (2014–2017) using independent repeated measures ANOVAs again with ANPP sensitivity as the response variable and fixed effects for Site and the drought type (natural or experimental). For both, we included Block as the random effect to account for repeated measures and for the comparison across drought years also included a Block–Period effect to account for plots being compared in one natural year vs. across multiple experimental drought years. In both 2012 vs. 2014 and 2012 vs. the 2014–2017 average, the interactions between Site and drought type were not significant, so we re-fit models without the interactive effect and were most interested in drought type effects over all sites (Table A1.8). To identify any legacy effects of drought, we evaluated the recovery years (2013 and 2018–2021) independently. As described above, we used a simple linear regression and ANOVA with pairwise comparisons to compare 2013 ANPP to the ANPP across all nine other years (Table A1.7). After the experimental drought (in 2018–2021), we compared ANPP in previously-droughted plots with ambient plots, both in the first year of recovery and averaged across all recovery years. We evaluated recovery with ANPP as the response variable and Site, Treatment, and their interaction as fixed effects in simple linear regressions and ANOVAs followed again by emmeans pairwise comparisons to check for differences in treatment effects within the different sites (Table A1.9). For all analyses, model assumptions were assessed graphically and response variables transformed as needed to best meet assumptions for normality and equal variance. All significance was assessed at $\alpha = 0.05$. Full results are included in the Supplemental Material, including types of transformations on response variables and output of all t-tests, ANOVAs, and pairwise comparisons.

2.4 Results

2.4.1 Drought characteristics

In 2012, the natural drought reduced growing season and annual precipitation by 35–40% for all sites (Fig. 2.2b, Knapp et al. 2015). Growing season precipitation reductions imposed by the experimental drought treatments were targeted at 66%, but actual reductions relative to each site's long-term precipitation records varied from 53 to 71% below average across the four years (or 46–61% reductions in annual precipitation compared to MAP for each site; Fig. 2.2b). Thus, both the magnitude of precipitation reductions and their duration (4-years vs. 1-year) were greater in the experimental than the natural drought. Limited plot-level soil moisture data were available only during the experimental drought, and these data confirm the effectiveness of precipitation reductions in reducing soil moisture levels (Fig. A1.1). Average growing season temperatures in 2012 were ~2.0˚C warmer than during 2014–2017 (ranging from + 1.59˚C at KNZ to + 2.22˚C at SGS) and 2012 growing season VPD was also significantly higher (mean = 0.49 kPa, ranging from 0.4 kPa at HPG to 0.61 kPa at HYS) than during the experimental drought years (Fig. 2.2b–d). Finally, the seasonality of the natural and experimental droughts varied as well. While the seasonal timing and duration of the 4-year experimental drought was consistent across all the grassland sites (treatments imposed from ~April 1– September 15), the seasonality of the 2012 drought varied substantially across the sites (Fig. A1.2). For the drier grasslands (HPG and SGS), the 2012 drought was most severe early in the year (March–May) whereas at HYS, the 2012 drought occurred primarily during the summer months (June–August), similar to the timing of the experimental drought (Fig. A1.2). The KNZ site was intermediate between these two patterns.

2.4.2 ANPP responses

In general, all drought years (2012 and 2014–2017) reduced ANPP at all four sites with the C_3 dominated HPG site typically responding less than the C_4 grasslands (Fig. 2.3). The 2012 pan-continental drought reduced ANPP the least (44%) at the C_3 dominated HPG site and the most (69%) at the SGS site (Fig. 2.3). These estimates exceeded the 25–55% reductions previously reported by Knapp et al. (2015), reflecting our updated estimates of ambient (nondrought) ANPP available for each site instead of the previous method of using long-term ANPP data from outside of the experimental area. During the first year of the experimental drought (2014), ANPP reductions during the experimental drought were much less than the 2012 drought – varying from 11 to 25% across the four sites. Even after four years of simulated drought, ANPP reductions ranged from only 4% at HPG to ~40% at KNZ. Thus, although ANPP at the C_3 grassland (HPG) responded significantly (Site–Period interaction $F_{3,203.09} = 11.992$, $p<0.0001$ and HPG pairwise $t_{148} = -5.757$, $p<0.0001$; Table A1.7) to the natural drought (44% reduction), we did not observe overall significant reductions at this site between ambient and droughted plots during the experimental drought years (Fig. 2.3, Table A1.6). In contrast, the response to experimental drought was significant for most years in all of the C4 grasslands, but reductions were generally less than in 2012 (Fig. 2.3b, Table A1.6). Thus, contrary to our expectation that multi-year experimental drought would impact ANPP more than a one-year natural drought, we found that ANPP was reduced to a much greater extent during the natural drought.

2.4.3 Relative ANPP sensitivity to natural vs. experimental drought

Because the four grasslands varied significantly in both ANPP and precipitation, we used a standardized metric, g m^{-2} reduction in ANPP per mm reduction in precipitation, for our assessment of drought sensitivity. Ecosystems, and especially grasslands, are known to differ in their sensitivity to drought (Huxman et al. 2004; Cherwin and Knapp 2012; Knapp et al. 2015; Zuo et al. 2022; Jaman et al. 2022), and the four grasslands we studied did indeed differ in drought sensitivity (g m^{-2} mm^{-1}) in response to the natural drought, the first year of the experimental drought ($F_{1,34.945} = 49.1447$, $p < 0.0001$; Table A1.8), and for the average of all experimental drought years ($F_{1,64.704} = 68.200$, $p < 0.0001$; Table A1.8). As expected from comparisons of absolute and relative ANPP responses (Fig. 2.3), drought sensitivity was consistently lower in response to the experimental drought (1st year and over all 4 years) than the natural drought ($F_{1,6} = 18.4066$, $p = 0.0051$; Fig. 2.4) but the relative ranking of drought sensitivity among the sites did not differ markedly (Fig. 2.4). In general, the C_3-dominated grassland was the least sensitive to drought and the two warmer C_4 grasslands were more sensitive. Of note, the drought sensitivity estimates for the simulated droughts were all within the range reported previously (Huxman et al. 2004) based on long-term ANPP-precipitation relationships. In contrast, the estimated drought sensitivity for the natural drought (which combined reduced precipitation and elevated temperatures and VPD) was greater than previously reported for three of the four grasslands (Fig. 2.4).

2.4.4 Post-drought recovery

Patterns of drought recovery were generally inconsistent when comparing the natural vs. experimental droughts. In the recovery year after the 2012 natural drought, only SGS showed significant changes in ANPP compared to long-term site averages with increased ANPP (Site–Period interaction $F_{3,182.70} = 4.2728$, $p = 0.0065$ and pairwise $t_{130} = 3.143$, $p = 0.0021$; Table

A1.7), compared to the long-term site averages (Fig. 2.5), while ANPP in the year after drought at KNZ, HYS, and HPG did not differ from their long-term means. In contrast, ANPP at KNZ and HYS remained reduced in the first recovery year after the 4-year experimental drought (Site–Treatment interaction $F_{3,111} = 7.3685$, $p = 0.0002$; KNZ pairwise $t_{111} = 3.780$, $p = 0.003$; HYS pairwise $t_{111} = 2.338$, $p = 0.0212$; Table A1.9), whereas ANPP at SGS was increased (SGS pairwise $t_{111} = -2.118$, $p = 0.0364$; Table A1.9) and at HPG did not differ between previously droughted and ambient plots (HPG pairwise $t_{111} = -0.725$, $p = 0.4701$; Table A1.9). When the entire 2018–2021 recovery period was assessed, only HPG shows marginal evidence of post-drought legacies impacting ANPP (Site–Treatment interaction $F_{3,112.01} = 3.0674$, $p = 0.0309$; HPG pairwise $t_{113} = -1.972$, $p = 0.0511$; Table A1.9), possibly driven by ANPP responses in 2020 (Fig. 2.3) which was the driest recovery year (Fig. 2.2). However, the lack of response during drought in this site makes this response difficult to attribute to the experimental drought treatment.

2.5 Discussion

Comparisons of ecological responses to natural meteorological anomalies vs. those simulated via controlled experiments can be challenging, particularly across multiple sites, but insights can still be gained (e.g., Peñuelas et al. 2007; Sandel et al. 2010, Yuan et al. 2017). Here, we took advantage of 10 years of drought research in four native grasslands that spanned a broad precipitation gradient and differed in species composition and many key plant traits (Griffin-Nolan et al. 2018a, b; Carroll et al. 2021). Each of these grasslands were exposed to a natural, pan-continental drought in 2012 followed two years later by an experimental drought (four years of growing season precipitation reduction). Key advantages of this comparison are that the natural drought was of similar severity for all grasslands (Knapp et al. 2015) as was the experimental drought (Carroll et al. 2021), the experimental drought was imposed identically at all sites, post-drought recovery was measured for both droughts at all sites with recovery periods equal to drought duration, and the focal response variable (aboveground net primary productivity, ANPP) was measured consistently and from the same plots over the entire 10-year period. Of course, there are also multiple caveats that must be acknowledged when comparing responses to these two droughts. Primary among these are the obvious differences in drought duration (one vs. four years), the high air temperatures and VPD that co-occurred with the natural drought but were not present during the experimental drought, and the more subtle differences in the seasonality of the droughts. Indeed, drought duration, atmospheric demand, and the seasonal pattern of water limitation during drought are all expected to impact ANPP responses and potentially post-drought recovery (Felton et al. 2020; Hajek and Knapp 2022; Gamelin et al. 2022; Wright and Collins 2024).

The key insights from this study are, first, that the 1-year 2012 drought reduced ANPP more than the experimental drought – and this was true for both the first year of the simulated drought and when drought impacts were averaged over the entire 4-year drought period (Fig. 2.3). Note that apart from the C_3 dominated HPG site, there were some individual years for each of the C_4 grasslands when differences in ambient vs. droughted plots were of a similar magnitude to the 2012 natural drought, but these were the exceptions rather than the rule (Fig. 2.3). This pattern occurred despite the experimental drought imposing greater reductions in precipitation inputs than the natural drought. This general conclusion was also evident when comparing previous independent analyses of these droughts (Knapp et al. 2015; Carroll et al. 2021), but the degree of divergence in ANPP reductions is now greater based on the decadal ANPP data available at each site. For example, Knapp et al. (2015) reported that ANPP was reduced by ~25–

50% from the 2012 drought, but our revised estimates are ~45–75% ANPP based on more accurate estimates of mean ANPP for each site (Fig. 2.3). Revised estimates of the 2012 drought impact differed most strongly at the HYS and SGS sites, while the ANPP reductions at the HPG and KNZ sites were similar. In contrast, estimates of ANPP reductions to the experimental 4-year drought (Fig. 2.3) ranged from very little reduction at HPG to ~40% ANPP reductions at KNZ, with these broadly similar to those reported previously (Carroll et al. 2021). Overall, these results support previous concerns that simulating drought via precipitation reductions alone can underestimate natural drought impacts because concurrent increases in air temperature and VPD are also not imposed (De Boeck and Verbeeck 2011; Novick et al. 2016; Kröel-Dulay et al. 2022; Wright and Collins 2024). Based on past complementary analyses for this grassland region, it is likely that increases in VPD will impact productivity more than warmer temperatures (Mowll et al. 2015; Konings et al. 2017).

It is worth noting that during the experimental drought, proportional reductions in graminoid ANPP were generally greater than total ANPP at HYS and HPG and less than total ANPP at SGS (and during recovery, we saw similar trends for these sites, Fig. A1.3), reflecting potential shifts in species composition during the 4-year simulated drought. When comparing proportional reductions in biomass separated by functional groups (C_3 or C_4 grasses, forbs, and woody plants when present), we noted greater reductions in C_4 grasses then C_3 grasses at the three C_4-dominated grasslands (KNZ, HYS, and SGS) and proportional increases in forb biomass at SGS and HPG in the last year of experimental drought (Fig. A1.4). However, previous analyses of community composition data by Griffin-Nolan et al. (2019) reported community shifts only from C_4 to C_3 grasses at HYS and SGS over the course of the four-year experimental droughts, with no observable effect of the experimental drought treatments at KNZ or HPG. During the single-year natural drought, there were small proportional reductions in C_3 grasses and forbs from 10-year functional group biomass averages that tended to be greater than reductions in total ANPP at HPG and SGS. However, at HYS, C_3 grasses increased modestly compared to 10-year biomass averages – which is not unexpected as this grassland was the only site where the 2012 natural drought reduced summer precipitation more than spring precipitation (Hajek et al. 2024). At KNZ, 2012 biomass data was only available as graminoid and total ANPP, and here both were reduced equally. The experimental drought had the greatest precipitation reductions in the summer months (Fig. A1.2), so differences in functional group responses to different timing of drought are not unexpected (Knapp et al. 2020; Hahn et al. 2021; Hajek et al. 2022).

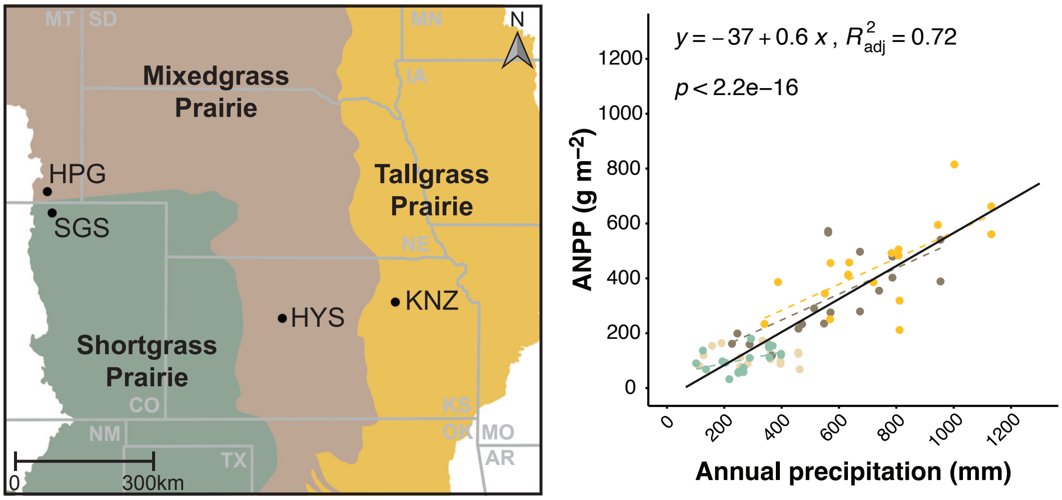
The second insight is that, despite the experimental drought underestimating the magnitude of ANPP reductions, relative differences in drought sensitivity among grasslands were similar when comparing the natural vs. simulated drought among the four sites. The Huxman-Smith model of ecosystem sensitivity to changes in precipitation predicted that the greatest sensitivity to drought, and the greatest variability among ecosystems in drought sensitivity, will occur where MAP < 1000 mm (Huxman et al. 2004), a pattern confirmed by Mauer et al. (2020). We observed a similar relative ranking of drought sensitivity among the 4 sites (all less with < 1000 mm MAP) based on both the natural and experimental drought (Fig. 2.4), with the C_3 dominated grassland (HPG) consistently the least sensitive. Many C_3 grasslands in North America rely on winter and early spring soil moisture and can be relatively insensitive to reductions in precipitation during the summer months (Frank 2007; Knapp et al. 2015, 2020).

It is also worth noting that the estimates of drought sensitivity from the 4-year simulated drought were quantitatively similar to the Huxman-Smith estimates (Huxman et al. 2004) whereas this sensitivity metric was generally higher for the natural drought (Fig. 2.4). The underestimation in sensitivity to simulated drought compared to the natural drought is likely because both the Huxman-Smith and simulated drought estimates of drought sensitivity are primarily driven by changes in precipitation. However, the natural drought additionally involved increased air temperatures and VPD (Fig. 2.2). Indeed, differences in this sensitivity metric between the simulated and natural drought diverged most in the two most mesic grasslands – consistent with prior analyses indicating that productivity in more mesic ecosystems will be more responsive to changes in VPD than in drier ecosystems, which are driven more by soil moisture (Novick et al. 2016; Kannenberg et al. 2024).

Finally, we found it difficult to draw any insights from comparisons of post-drought recovery patterns after the 1-year vs 4-years drought. Previously, Griffin-Nolan et al. (2018a, b) reported that legacy effects from the 2012 drought had both positive and negative legacy effects on productivity post-drought. At the C_3 dominated site (HPG), ANPP did not recover in the first year post-drought (suggesting a negative drought legacy) whereas the C_4 sites fully recovered, with ANPP at KNZ showing a slight positive drought legacy impact (higher ANPP in drought plots vs. ambient plots) in 2013. Based on our revised estimates of mean ANPP for each site, similar post-drought recovery patterns were observed in our reanalysis (Fig. 2.5) although the positive legacy of the 2012 drought at KNZ was no longer evident. Comparing the first year of recovery after the 4-year simulated drought (2018) to the natural drought is complicated by substantial differences among sites in annual precipitation in 2018 vs. 2013 (Fig. 2.2). In the first year after the 4-year simulated drought, post-drought legacy effects were negative at KNZ and HYS, positive at SGS and not evident at HPG, with all sites displaying largely idiosyncratic patterns of recovery throughout the 4-year post-drought period (Figs. 2.3, 2.5). The general conclusion of Griffin-Nolan et al. (2018a, b) that there is evidence for both positive and negative drought legacy impacts among the four grasslands is also supported by recovery dynamics after the experimental drought. However, it is clear that the determinants of drought recovery of ecosystem function are varied, likely site specific, and will require additional study to more fully understand this aspect of ecosystem resilience (Sala et al. 2012; Vilonen et al. 2022).

In conclusion, our results underscore the limitation of manipulating precipitation and soil moisture as an approach for quantifying drought impacts on ANPP in ecosystems. Previous authors have suggested that passive precipitation reduction shelters may underestimate drought impacts by 53% (Kröel-Duley et al. 2022); our results were consistent with this magnitude of underestimation. Further, with trends of increasing VPD associated with warming, the magnitude of such underestimates may increase in the future. However, there are likely many interactions between decreasing soil moisture and increasing VPD during drought that required further exploration (Novick et al. 2024). It is possible, for example, that in dry ecosystems where soil moisture is extremely low during drought and primary producers become physiologically inactive, the impact of increasing VPD may be minimal relative to more mesic ecosystems (Novick et al. 2016; Xu et al. 2023; Kannenberg et al. 2024). If future experiments can manipulate VPD and soil moisture separately (Wright and Collins 2024), or parse them independently (Roby et al. 2020; Kannenberg et al. 2024), estimates of both the independent and combined impacts of increased VPD and decreased soil moisture during drought will be possible. However, even with the shortcoming of experimental manipulations underestimating the magnitude of drought impacts, such experiments can still provide valuable insight into the relative responses of ecosystems to reduced soil moisture, which remains a key aspect of understanding droughts.

2.6 Figures



Site	Grassland Type	MAP (mm)	GSP (mm)	MAT (˚C)	GST (˚C)	ANPP (g m^{-2})
KNZ	Tallgrass	856.8	591.3	12.5	21.0	487.0
HYS	Mixed	614.6	440.1	12.4	20.9	349.8
HPG	Mixed	385.1	275.9	7.6	14.5	103.8
SGS	Shortgrass	335.1	244.1	8.3	15.7	106.2

Figure 2.1. Site locations, characteristics, and ANPP sensitivity to annual precipitation at each of the four grasslands. Sites varied in their sensitivity of ANPP to interannual variability in precipitation (top right), shown by dashed lines for each site that showed at least marginally significant slopes (KNZ - gold, HYS - tan, and SGS - green; Table A1.1) and the solid black line showing the linear regression across all four sites. Climate characteristics of each site (bottom table) are long-term averages (1990-2020) for ambient mean annual precipitation (MAP), growing season (April 1– Sept. 15) precipitation (GSP), mean annual temperature (MAT), and growing season temperature (GST) (see Tables A1.2-A1.3 for 2012-2021 annual MAP, GSP, MAT, and GST as well). ANPP values for each site are the 10-year average (of ambient plots) for each site over the course of the study (2012-2021). Map shows approximate site locations of each grassland in the United States, with state borders shown in gray lines and state labels in gray text (MT – Montana, SD – South Dakota, MN – Minnesota, CO – Colorado, NE – Nebraska, IA – Iowa, KS – Kansas, MO – Missouri, NM – New Mexico, OK – Oklahoma, TX – Texas, and AR – Arkansas; adapted from Carroll et al. 2018).

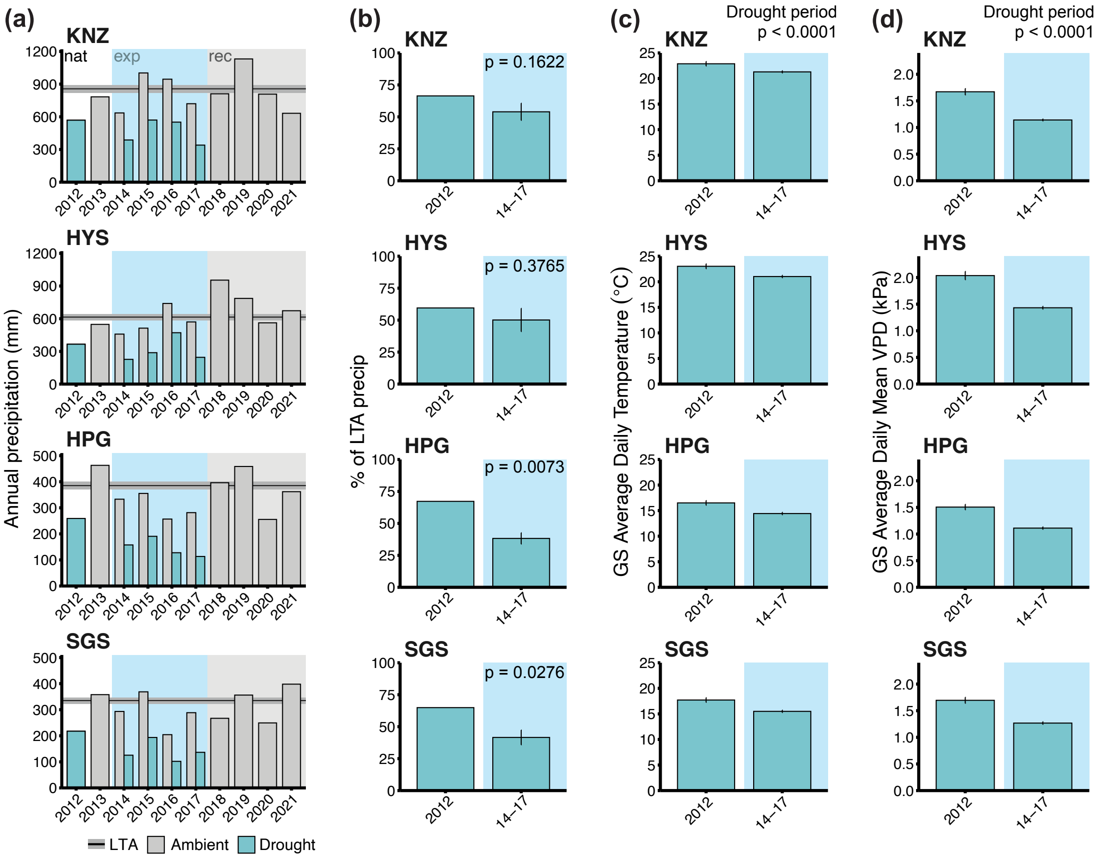


Figure 2.2. Drought conditions during the natural (2012) and experimental (2014-2021) drought periods (also see Table A1.2-A1.4 for yearly climate variables at year site). **(a)** Annual precipitation (mm) at each site for the natural drought years in 2012 and recovery in 2013 (white background), during the experimental drought years (blue background) in control/ambient plots and droughted plots, and for experimental recovery years (2018-2021; gray background shading. Each site has horizontal lines showing the 30-year MAP with ±1 SE gray shading. **(b)** Percent reductions in precipitation compared to long-term averages (LTA) for each site. Reductions for the natural drought year were compared to the average across experimental drought years using one-sample t-tests (Table A1.5). **(c)** Average daily temperatures during the growing season (GS) were significantly higher for the natural drought across all sites. **(d)** Daily mean VPD's during the GS were also higher across all sites. Simple linear regressions and ANOVAs were used to assess effects of site and drought period (natural vs. experimental) for temperature and VPD (not including interaction effects since they were non-significant, see Table A1.5 for details).

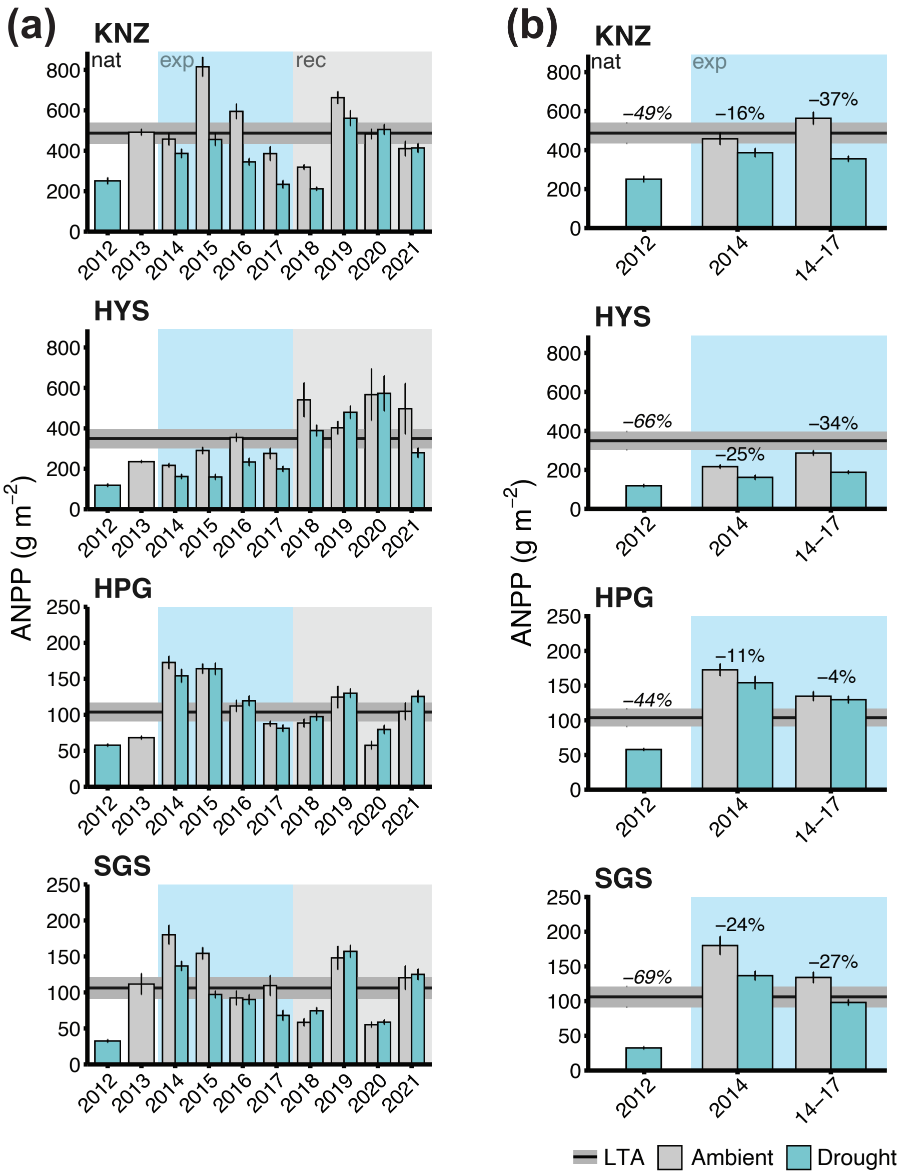


Figure 2.3. (a) ANPP (mean ±1 SE) at each site across all 10 study years. Background shading indicated the drought periods: white – natural drought/recovery years, light blue – experimental drought years, and gray – experimental recovery years. 10-year average ANPP for each site is shown with the horizontal black line (mean) with gray shading (±1 SE). **(b)** The natural vs. experimental drought ANPP responses and reductions (%) compared to either the 10-year ANPP average (horizontal lines and italicized numbers) for 2012 (white background) or to ambient plots during the drought experiment years (blue background; for full comparisons and statistics, see Tables A1.6-A1.8).

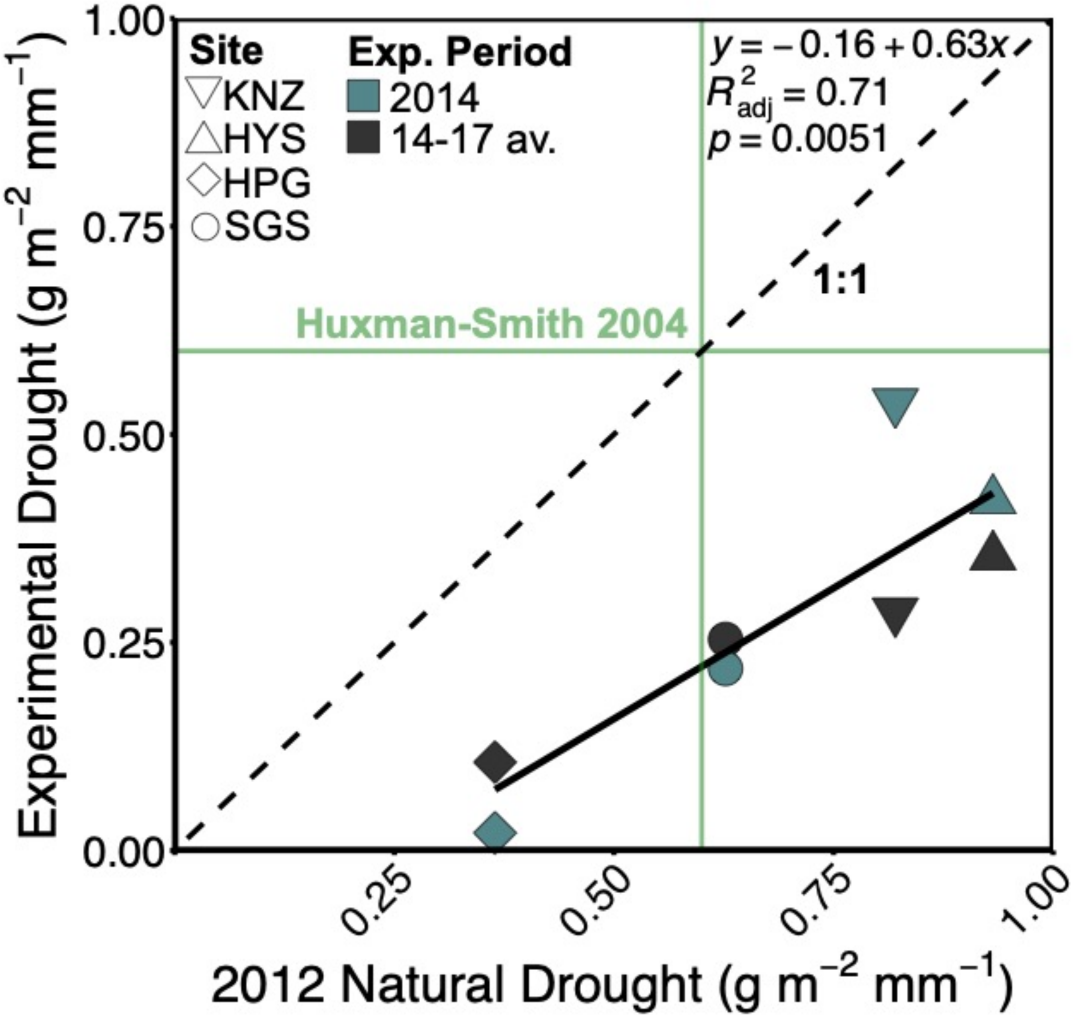


Figure 2.4. ANPP sensitivity (g m^{-2} mm^{-1}) to natural and experimental drought for each site comparing sensitivity to the 2012 drought and the experimental drought for both the first year of experimental drought (black points) and the average of the four experimental drought years (blue points). For our sites, ANPP sensitivity is expected to be no more than 0.6 according to Huxman, Smith, et al. (2004). For the experimental drought, all sites fall under the max sensitivity (green horizontal line), but for the natural drought, three of the four sites had greater sensitivity than previously reported (green vertical line).

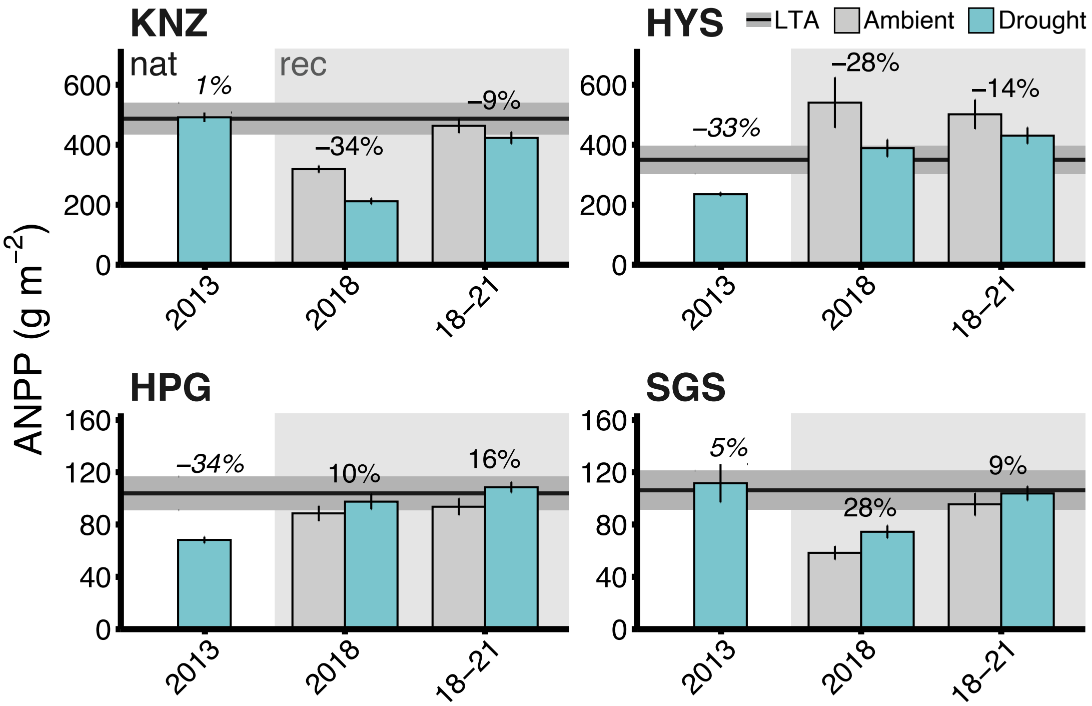


Figure 2.5. ANPP (mean ±1 SE) responses and percent reductions or increases during recovery after natural drought (2013 recovery year from 2012 natural drought – white background) and the experimental drought (2014-2017 drought with recovery in the first year (2018) or averaged across all recovery years (2018-2021) – gray background). Horizontal black lines show the 10-year ANPP averages for each site (± 1 SE gray shading). Percent reductions are shown comparing 2013 ANPP to the 10-year average (horizontal lines and italicized numbers) and 2018-2021 reductions in droughted plots compared to control/ambient plots (for full comparisons and statistics, see Table A1.9 – note that plots show percent reductions for each site vs. their 10-year averages but statistics compare 2013 to only 2012 & 2014-2021 9-year averages).

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CHAPTER 3: SUBTLE DIFFERENCES IN SPRING SOIL MOISTURE CAN SUBSTANTIALLY INFLUENCE ANNUAL PRODUCTIVITY IN A SEMI-ARID GRASSLAND[2]

3.1 Summary

In the C_4-dominated semi-arid grasslands of the western Great Plains (Colorado, USA), spring soil moisture (soil volumetric water content, $Soil_{VWC}$) is thought to be a critical determinant of above-ground net primary production (ANPP) and carbon cycling overall. However, because evidence for this is based on observational studies, we attempted to test this sensitivity by experimentally reducing spring (May-June) $Soil_{VWC}$ with standard drought shelters. Our goal was to reduce rainfall inputs from May to early July in a native grassland dominated by C_4 *Bouteloua spp* and assess ANPP and related carbon cycle responses. Although we were able to reduce ambient rainfall inputs directly into the plots, spring precipitation was unusually high (~40% above average) in the year (2021) of this experiment and our treatments had negligible impacts on $Soil_{VWC}$. Indeed, the drought shelters were able to reduce $Soil_{VWC}$ below ambient levels for only two weeks, after a large natural precipitation event (~65 mm) fell in late June. As expected, by mid-July, we could detect only minor impacts of our treatments on soil CO_2 efflux and canopy greenness, and no effect on ANPP, consistent with $Soil_{VWC}$ remaining at non-limiting levels throughout most of the first half of the growing season. Despite the seemingly ineffectiveness of the spring drought treatments, we challenged these plots with an experimental deluge (60 mm of water addition) after the drought shelters were removed. Surprisingly, in those plots subjected to the spring drought treatment we measured significant reductions in soil CO_2 efflux immediately after the experimental deluge as well as reduced

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[2] Condon KV, Knapp AK. Subtle differences in spring soil moisture can substantially influence annual productivity in a semi-arid grassland. Under consideration at *Ecosphere*.

canopy greenness throughout much of the remainder of the growing season. Moreover, end of season ANPP was reduced by 32%, and regrowth after grazing (simulated at midseason) was reduced by 45% in the treatment with only minor reductions in Soil_{VWC} in the spring. Our largely serendipitous results confirm the strong sensitivity of this grassland to alterations in early season rainfall inputs, even during a wet spring when measurable impacts on soil moisture are minimal.

3.2 Introduction

Precipitation and, by extension, soil moisture are well-established determinants of productivity and ecosystem services (forage production) in grasslands globally, and particularly in arid and semi-arid ecosystems (Sala et al. 1988 & 2012, Fay et al. 2003, Maurer et al. 2020, An et al. 2024). But despite strong overall positive relationships between ANPP and precipitation within and across grasslands, there is often much variation unexplained by precipitation alone (Oesterheld et al. 2001, Mowl et al. 2015, Knapp et al. 2017). For example, ANPP can vary >2-fold with the same annual precipitation for any two individual years (Lauenroth and Sala 1992, Briggs and Knapp 1995, Nippert et al. 2006, Fahey & Knapp 2007, Felton et al. 2019), despite highly significant regressions between ANPP and precipitation overall (Huxman et al. 2004, Maurer et al. 2020, Felton et al. 2021, Chapter 2). There are many potential factors that can explain such interannual variation including but not limited to – differences in nutrient availability and community composition (Avolio et al. 2014, Gherardi and Sala 2015, La Pierre et al. 2016), variations in temperature and VPD among years (Mowll et al. 2015, Konings et al. 2017), differences in the size, timing and pattern of individual precipitation events (Hajek and Knapp 2022, Griffin-Nolan et al. 2018, Felton et al. 2020, Feldman et al. 2024), the presence of absence of deluges (unusually large individual rain events; Post and Knapp 2020, Hoover et al.

2022) and legacy effects of previous years' precipitation (Oesterheld et al. 2001, Sala et al. 2012, Griffin-Nolan et al. 2018, Vilonen et al. 2022).

In the semi-arid grasslands of the western US Great Plains, the importance of early season soil moisture as a determinant of annual productivity is particularly well-established. Previously, Parton et al. (2012) evaluated both precipitation timing and event size effects on net ecosystem productivity in the shortgrass steppe and determined that precipitation from May to June, and large precipitation events overall, had a strong positive impact on carbon uptake and aboveground productivity. Similar patterns were also identified by Hoover et al. (2021) in this grassland type over their 36-year analysis of precipitation-productivity (PPT-ANPP) relationships. Indeed, a management tool, Grass-Cast, which is designed to forecast forage production across much of the Great Plains region, is largely based on the importance of mid-April (for Southern Great plains) or mid-May (for Central and Northern Great Plains) to early June soil moisture and precipitation patterns (Hartman et al. 2020). The accuracy of Grass-Cast estimates, based on observational long-term PPT-ANPP relationships, ranges from 60-80% by mid-June (Hartman et al. 2020, Elliott 2022). Our original goal was to test this foundational knowledge experimentally, by manipulating spring precipitation inputs and soil moisture, and then assess how ANPP, canopy growth, and soil CO_2 flux responds. This would allow us to control for potential confounding factors and assess experimentally how sensitive ANPP in this grassland is to alterations in early season soil water availability. In addition, we sought to assess how such differences in spring soil moisture might impact responses of this semi-arid grassland to midseason large deluge events (Post and Knapp 2020 & 2021, Post et al. 2021). The latter goal was motivated by the expectation that these large events will increase in frequency with climate change (Tabari 2020, Gulev et al. 2021).

Our approach was to reduce spring soil moisture levels using precipitation interception infrastructure that is well-established (drought shelters; Gherardi and Sala 2013, Loik et al. 2019, Post and Knapp 2020). But, and as aptly expressed by Tyree (1983) four decades earlier "…weather conditions could not be arranged to meet experimental requirements". Due to unusually high natural rainfall during the spring of 2021 (~40% greater than long-term average growing season precipitation, Fig. 3.1), our ability to reduce spring precipitation inputs to levels that reduced soil moisture (measured as volumetric soil water content) in treatment plots was challenged due to lateral water flow. Differences in measured soil moisture beneath drought shelters vs. control plots were minimal despite trenching the perimeter of plots. Overall, soil moisture was rarely reduced even though we certainly excluded some unknown fraction of natural precipitation. This resulted in treatments that could best be described as plots with very high vs. high soil moisture. Rather than abandoning this experiment, we continued the remainder of our measurements as planned. But our goal shifted to determining if the presence of the drought shelters would have detectable impacts on ecosystem structure and function throughout the rest of the growing season. We were particularly interested in determining if subtle differences in spring soil moisture levels effect responses to 1) an experimental deluge later in the season and 2) aboveground defoliation at mid-season (a surrogate for one aspect of large herbivore grazing) might be affected by these subtle differences in spring soil moisture levels. We anticipated that we would not detect any impact of our treatment given that even our reduced soil moisture levels were still well-above average for the spring in this grassland (Hoover et al. 2022, Post and Knapp 2021, Saxton and Rawls 2006), but were surprised to find several differences in ecosystem responses to the mid-season deluge with differing spring histories.

3.3 Methods

3.3.1 Site Descriptions

Our study took place at the Central Plains Experimental Range (CPER), a US Department of Agriculture – Agricultural Research Service site in northern Colorado (40.8055ºN 104.7139ºW, elevation = 1,625 m). The site is dominated by native shortgrass steppe (co-dominated by C_4 grasses *Bouteloua gracilis* and *Bouteloua dactyloides*), a biome that originally covered ~20 million ha of land in the rain shadow of the Rocky Mountains (Holechek et al. 1998). At the northern extent of its range, the climate at the CPER is cool and semi-arid. Annual precipitation averages 341.5 mm, and 245.7 mm for the growing season (April 1 – September 15) and the mean annual temperature is 7.6 ºC (14.5 ºC during the growing season). Soils at the CPER are generally coarse textured (ranging from 40-60% sand, Singh et al. 1998) and field capacity for soil water is ~27% volumetric water content (VWC) with previous studies indicating that this grassland is not water-limited at soil moisture levels >30% (Hoover et al. 2022). Annual aboveground net primary production (ANPP) is low, averaging between 50 and 100 g m^{-2} depending on the topographic position (ridges to swales, Hoover et al. 2021).

In 2021, the area received 343.2 mm of growing season precipitation (i.e., an equivalent amount of precipitation to mean annual precipitation; Fig. 3.1). In addition, a historically rare deluge event occurred at midseason (~65 mm on June 24, >99th percentile of past rain events, Fig. 3.1). As a result, soil volumetric water content ($Soil_{VWC}$) was at or above ~30% for much of the growing season (Fig. 3.2), indicating that this was an anomalously wet year for the site.

3.3.2 Experimental Design and Treatment

We manipulated spring rainfall reaching experimental plots beginning May 2, 2021. We established 40 1 m^2 plots, each bordered with aluminum flashing 0.25 m away from experimental plot edges. This flashing was partially buried (~8 cm aboveground and ~12 cm belowground) to limit overland water flow. Ten plots were fully covered with clear polycarbonate roofs to reduce soil moisture in the spring and early part of the growing season by eliminating direct precipitation inputs. These rainout shelters were 2.44 × 3.05 m in size and remained in place through July 13, 2021. Thirty plots were left uncovered. Roofs were installed ~1 m above ground-level and angled to direct water into gutters and drainage tubes that diverted water away from all plots. Previous research suggests that such roofs are an effective way to redirect water away from plots while minimizing any effects on light availability or microclimates (Gherardi and Sala 2013; Loik et al. 2019; Post and Knapp 2019; Griffin-Nolan et al. 2021; Chapter 2).

After the roofs were removed in July, we imposed an experimental deluge treatment (60 mm of simulated rainfall) to the previously covered plots (n = 10) and 10 of the ambient unmanipulated plots. Based on previous studies of deluge responses in the shortgrass steppe, the timing and size of our deluge addition was expected to stimulate most ecosystem responses during more typical precipitation years (Post & Knapp 2020 & 2021, Hoover et al. 2022). We added the deluge by watering with a handheld garden wand equipped with a flow meter (Great Plains Industries, Wichita, Kansas) to deliver 60 mm of water (potable, to insure low nitrogen inputs) from adjacent holding tanks. We applied our deluge over two days (July 15-16, 2021) to facilitate effective soil water infiltration and eliminate runoff. All plots were randomly assigned to the combination of spring drying and deluge addition treatments, with 10 plots assigned to the drier spring and deluge addition treatment (Dr + De) and 10 plots assigned to ambient spring and deluge addition (A + De), which we compared to the remaining 20 ambient (A) plots.

3.3.3 Measured responses

In all plots (n = 40), we measured 20 cm soil moisture ($\mathrm{Soil}_{\mathrm{VWC}}$), canopy greenness, soil nutrient availability, and aboveground net primary production (ANPP). Half of the plots were also equipped with soil respiration collars to measure soil CO_2 efflux ($\mathrm{Soil}_{\mathrm{resp}}$), and in a subset of these plots (n = 12) we also measured the depth distribution of soil moisture from 0-100 cm in 10 cm increments. Climate variables (precipitation and temperature) were aggregated from available site data from USDA or a nearby Soil Climate Analysis Network (SCAN) site's daily measurements.

Soil moisture, canopy greenness, and soil respiration were measured approximately weekly throughout the growing season, with more frequent measurements after the experimental deluge addition. Soil moisture to a depth of 20 cm was measured in each plot at least 25 cm away from any plot edges using a time-domain reflectometry probe (Campbell Hydrosense II). PVC access tubes were previously installed to 90-100 cm depths in twelve plots (n = 6 in ambient plots and 3 for each of the deluge addition treatments) to measure 0-100 cm soil moisture at 10 cm increments using a Diviner 2000$^{\mathrm{TM}}$ soil moisture probe (Sentek Pty Ltd.). A site-based calibration was used for this instrument (Hoover at al. 2022, Jabro et al. 2005). Linear interpolations (R package imputeTS, Mortiz and Bartz-Beielstein 2017) were used to integrate measurements by depth (to 5 cm resolution) and over time (daily). We assessed changes in canopy greenness using repeat photography, where a 0.25 m^2 undisturbed portion of each plot was photographed from directly above. Photos were cropped in Adobe Photoshop to the inside boundary of the 0.25 m^2 quadrat and then analyzed using the R package EBImage (Pau et al. 2010) to calculate the average green chromatic coordinate (GCC). The GCC, or the ratio of greenness relative to total brightness of the photo (G/(R+G+B)), was assessed for each pixel and then the average of all pixels taken to obtain a mean GCC for each image. By using the GCC index, any differences in lighting or shadows are accounted for in the ratio, so we do not expect any impact of our drought shelters on greenness measurements. We used a LI-6400XT (LI-COR) equipped with a soil respiration chamber to measure soil CO_2 efflux ($Soil_{resp}$) between 10 am-1 pm on each measurement day, approximately once a week, and always on the same day as 20 cm soil moisture measurements. Permanent PVC collars of 10 cm diameters were installed in half of the plots ($n = 10$ in ambient plots, $n = 5$ for each of the deluge addition treatments), with ~2 cm of the collar remaining aboveground to place the soil respiration chamber on for each measurement. Collars were installed originally in areas of bare soil, and any new plant material that grew in collars was clipped and removed prior to each measurement. Soil temperature at 10 cm depth was also measured at the same time outside of each collar.

Aboveground biomass, as an estimate of ANPP (Fahey and Knapp 2007), was measured two times during the growing season and soil nutrient availability once over a 60-day period. Aboveground biomass was harvested in each plot in the mid- and late-growing season (before the deluge addition in July and again in early September). ANPP was estimated by clipping all aboveground plant biomass from a 0.2×0.5 m^2 subplot in each plot and sorted by plant functional groups (C_3 grasses, C_4 grasses, annual grasses, and forbs) in the field. Samples were sorted to remove dead plant material from previous years before being dried at 60 ºC for 2 days and then weighed to the nearest 0.01 g. The July harvest subplots were used in two ways: (1) to provide a mid-season estimate of ANPP in response to the early season treatments and (2) by harvesting these exact subplots again in September (along with the additional new September subplots), we estimated the potential for ANPP to recover (plants to regrow) after simulated mid-season grazing. We recognize that harvesting all aboveground biomass is not a perfect surrogate for grazing, but we hypothesized that that the ability to regrow after biomass harvest would be related to post-grazing regrowth. Nutrient availability was estimated using Western Ag Plant Root Simulator (PRS$^{®}$) probes installed two days before the deluge addition in July for a total of 60 days. Our intent was to determine if this large pulse of soil water altered nutrient levels in the soil. Three pairs of probes (with each pair including one for anions and one for cations) were installed in each plot, removed after 60 days, and analyzed by the manufacturer (https://www.westernag.ca/innovations/technology/analysis_units).

3.3.4 Statistical Analysis

Analyses for all responses were completed in R version 4.4.1, with all significance assessed at $\alpha = 0.05$. For each response, we removed outliers with Bonferroni $p < 0.05$ (< 1 % of data were outliers, Table A2.1) prior to analysis. Assumptions for normality and variance were assessed graphically and response variables transformed as needed to best meet model assumptions before continuing analyses.

For continuously measured variables, we analyzed differences between treatments at each sampling date using linear mixed effects models and repeated measures analysis of variance (ANOVAs) with soil moisture, GCC, or soil respiration as the response variables, treatment and sampling date as fixed effects, and plot as a random effect to account for repeated measurements on the same experimental units over time. When the treatment–date interaction effect was significant, we used Tukey-adjusted pairwise comparisons to check for differences between treatments at each date. If the interaction term was not significant, we included only the additive effects and checked pairwise comparisons of treatment effects averaged over time. Since these responses are all expected to change over the course of the growing season with changes in temperatures, rainfall, etc., we were not interested in differences over time without the effect of treatments (i.e., the significance of the date main effect alone would not be surprising).

To more directly assess the effect of the deluge addition, we also analyzed each continuously measured variable for specific response periods. Daily measurements were averaged over four periods: (1) pre-deluge – from the beginning of the growing season until the natural deluge on June 24, (2) natural deluge response – from June 25 to July 15 – the dates between when the natural deluge fell and before our experimental deluge was added, (3) experimental deluge response – from July 16 to August 6 – starting the day of our experimental deluge addition through the date where pairwise comparisons for 20 cm soil moisture no longer differed between the deluge and ambient treatments, and (4) post-deluge – August 7 to the end of the growing season (Table 3.1). Daily measurements for each response variable were averaged within each of our four deluge periods (n = 3 sampling dates for each response variable during the natural deluge response period and n= 5-7 dates for the experimental response period) and differences in treatment averages assessed again using linear mixed effects models and repeated measures ANOVAs for each response variable (soil moisture, GCC, or soil respiration) regressed against fixed effects for treatment and deluge period (pre-deluge, natural and experimental deluge response periods, or post-deluge), and again including plot as a random effect for repeated measures.

When treatment – deluge period interaction effects were significant, we used Tukey-adjusted pairwise comparisons to determine treatment differences within each deluge period. We also created separate simple linear regressions to compare treatment effects on ANPP growth by the end of the season (September) and on ANPP regrowth (July – September), with ANPP (g m^{-2}) as the response variable and treatment as the fixed effect. Similarly, soil nutrient availability was analyzed using simple linear regressions with rate (µg Nutrient 10 cm^{-2} 60 $days^{-1}$) as the response variable and treatment the predictor. We used ANOVAs and Tukey-adjusted pairwise comparisons to determine treatment differences for each of the simple linear regressions.

3.4 Results

3.4.1 Environmental and Shelter Effects

The effects of the rainout shelter roofs on soil moisture ($\mathrm{Soil}_{\mathrm{VWC}}$) were not evident in the spring, until the natural deluge occurred (Fig. 3.2a). Indeed, our effort to reduce $\mathrm{Soil}_{\mathrm{VWC}}$ by deflecting precipitation was most evident following the natural deluge, but even here, we detected increased soil moisture in the plots with roofs, indicating that the rainout shelters were not as effective as expected (Fig. 3.2a-b). However, the magnitude of increases in soil moisture were much higher in response to the natural deluge for the ambient treatments at both shallow and deeper depths (Fig. 3.2c-d).

3.4.2 Treatment Responses

The experimental deluge addition significantly increased $\mathrm{Soil}_{\mathrm{VWC}}$ and differences among the three treatments (A = ambient, Dr + De = drier spring + deluge, and A + De = ambient spring + deluge) persisted for ~3 weeks post-experimental deluge. Shallow soil moisture (0-20 cm) increased in both deluge addition treatments to a similar level during the experimental response period (Fig. 3.2c), but at greater depths (Fig. 3.2d), a legacy of the spring rain exclusion treatment was evident such that $\mathrm{Soil}_{\mathrm{VWC}}$ was higher in the A + De compared to the Dr + De treatment, with the latter not differing from ambient (A) $\mathrm{Soil}_{\mathrm{VWC}}$. These responses are also evident in how soil moisture varied with depth and time (Fig. 3.2b). The drier spring legacy effect continued through the end of the growing season ("Post" period), whereas differences in spring drying were more evident in deeper $\mathrm{Soil}_{\mathrm{VWC}}$ measures than in more shallow soils (Fig. 3.2c-d).

Canopy greenness (GCC) and soil respiration ($Soil_{resp}$, μmol CO_2 m^{-2} s^{-1}) were measured continuously over the growing season, approximately 1-2x per week with more frequent measurements taken following the deluge addition. Similar to $Soil_{VWC}$ patterns, there was little response in GCC to spring drought treatment until after the natural deluge (Fig. 3.3a). Conversely, $Soil_{resp}$ was the only response that showed a clear reduction in the pre-deluge period, with the spring drying treatment leading to reduced CO_2 flux (Fig. 3.3b). During the natural deluge response period, GCC was less stimulated in the spring drought treatment, whereas there was a substantial increase in greening in the ambient treatment (Fig. 3.3a), again following the responses of $Soil_{VWC}$ (Fig. 3.2). In contrast, $Soil_{resp}$ increased during the natural deluge response period, but this did not lead to either treatment being greater than the other (Fig. 3.3b). Canopy greenness in response to the experimental deluge revealed unexpected effects of the spring drying, as GCC was lowest in Dr + De throughout the experimental deluge response period compared to both ambient (A) and A + De treatments (Fig. 3.3a). As GCC in all treatments decreased towards the end of the growing season, the deluge effect remained evident in the A + De treatment, whereas the A and Dr + De treatments senesced relatively quickly and to a similar extent post-deluge (Fig. 3.3a). $Soil_{resp}$ during the experimental deluge response period also showed little response in the Dr + De treatment, but $Soil_{resp}$ in the A + De treatment was significantly greater (Fig. 3.3b). Post-deluge $Soil_{resp}$ showed similar trends, though these differences were no longer significant.

Surprisingly, ANPP responded differently to the spring drying and deluge addition treatments at mid- and late-season. The brief period of reduced $Soil_{VWC}$ during the natural deluge response period did not result in differences in ANPP between treatments at mid-season, however, both ANPP regrowth and end of season ANPP (total growth) in the Dr + De treatments were significantly reduced compared to the A + De treatment. This indicates that the legacy of precipitation reductions, despite being mostly ineffective at reducing Soil$_{VWC}$ and having little apparent impact at midseason, was clearly evident later in the season in response to the experimental deluge (Fig. 3.4).

Because changes in Soil$_{VWC}$ and drought can influence nutrient availability (particularly soil N; Birch 1958, de Vries et al. 2016), we targeted measurements of soil nutrients for the latter half of growing season after the rainfall reductions had been imposed. Availability was measured over 60 days – starting a few days before our experimental deluge addition and ending ~2 months after. Of the multiple nutrients assessed, difference in NO_3 were most striking (levels of NH_4 were below detection limits for most probes). Availability of NO_3 was significantly higher for both deluge addition treatments compared to the ambient treatment that had not received a deluge (Fig. 3.5). Additionally, the average nitrate availability in the Dr + De treatment trended towards being higher than in the A + De treatment, though responses were highly variable and not statistically significant ($p = 0.2511$, Fig. 3.4).

3.5 Discussion

The impacts of changing precipitation regimes, including seasonality, and extremes in precipitation (droughts and deluges) have been shown to be particularly important in semiarid and dryland ecosystems (Noy-Meir 1973, Sala et al. 1992, Reynolds et al. 2004, Post and Knapp 2020 & 2021, Lu et al. 2021, Hajek and Knapp 2022, Sun et al. 2022, Knapp et al. 2024). In this study, we attempted to assess how reductions in spring precipitation and soil moisture (Soil$_{VWC}$), posited to be a key determinant of the carbon cycle in this C_4-dominated semi-arid grassland, would influence ecosystem responses later in the season to an experimental deluge. However, high levels of ambient precipitation, particularly early in the growing season, rendered our treatments (drought shelters) largely ineffective at reducing Soil$_{\text{VWC}}$. Indeed, over the ~10 weeks that the drought shelters were in place, there were only two weeks when Soil$_{\text{VWC}}$ was below 30% (a conservative threshold for water limitation of ecosystem processes in this grassland; Hoover et al. 2022, Post and Knapp 2021, Saxton and Rawls 2006). Even during these two weeks, Soil$_{\text{VWC}}$ remained >20%, which would be considered typical for a year with normal precipitation (Post and Knapp 2021). Thus, we expected to see little impact of our spring treatment later in the year after drought shelters were removed. However, it appears that while the amount of precipitation removed from treatment plots (unquantifiable due to unknown amounts of rain blowing in during storms) was not sufficient to impact Soil$_{\text{VWC}}$ (Fig. 3.2), this reduction was evident in how the grassland responded to a mid-season deluge in a variety of ways. Thus, the importance of the overall early season water balance in this grassland, while not manifested in patterns of Soil$_{\text{VWC}}$, was apparent in multiple measures of ecosystem functioning – even in this most unlikely year. Indeed, our results suggest that other ways to quantify soil water availability, rather than volumetric water content, may be needed during above average precipitation years in this grassland.

The importance of spring soil water availability was most striking when focusing on the A + De and Dr + De treatments. For example, in the response of Soil$_{\text{VWC}}$ to the experimental deluge at deeper soil depths (Fig. 3.2b, d), note that soil moisture increased less in the previously “droughted’ treatment compared to A + De. This is evidence that overall water storage in the soil profile was reduced by the drought shelters even if Soil$_{\text{VWC}}$ did not respond during the exclusion period. Drying in the deepest soil layers may have been due to redistribution from deeper layers via capillary movement or hydraulic lift (which has been reported in *Bouteloua* species previously; Armas et al. 2012). However, since most plant roots in this system are limited to the upper 30 cm of soil, we do not believe differences in deep Soil_{VWC} are a primary mechanism of the legacy effects in ecosystem responses that we identified.

Subsequent responses to the precipitation changes were evident in the Dr + De treatment as reduced canopy greenness, soil CO_2 flux, N availability, annual ANPP, and in late season ANPP as regrowth after simulated grazing. Our results thus add experimental support to observational studies that have identified the key role that early season precipitation plays in multiple aspects of ecosystem functioning in the shortgrass steppe (Parton et al. 2012, Hoover et al. 2021).

Large precipitation events and deluges have also been posited to strongly impact ecosystem functioning (primarily ANPP) in this grassland (Sala et al. 1992, Hoover et al. 2022, Cherwin and Knapp 2012, Parton et al. 2012, Post and Knapp 2019 & 2021). Past studies of the impacts of deluge events (> 40 mm) in the grassland indicated that the shortgrass steppe is most responsive to deluges at midseason (relative to early or late season events, Post and Knapp 2020) and that ecosystem responses do not appear to saturate as deluge size increased to as much as 120 mm or twice the size of the deluge we imposed (Post and Knapp 2021). Thus, the responses we measured, even in an unusually wet year, are consistent with past research. For example, comparing the Ambient (A) to the deluge (A + De) treatments (these differed only in the addition of the 60 mm deluge event) indicates that this grassland responded positively in soil CO_2 flux and soil N, canopy greenness, and late season ANPP (Fig. 3.3-3.5) even in a year with well-above average precipitation (~40%). And even after a natural deluge occurred just 3 weeks prior to the experimental deluge (Fig. 3.2). This suggests that the capacity of this semi-arid grassland to respond to this type of climate extreme can now be extended from below average precipitation years (Post and Knapp 2019) to average (Post and Knapp 2020) to above average precipitation years (this study). Such broad sensitivity to precipitation event size in relatively arid ecosystems is consistent with recently identified global patterns (Feldman et al. 2024).

Finally, the strongest biotic response to the treatments was the late season regrowth potential of the grassland. The measurement of ANPP a second time in plots harvested at midseason provides some insight into how this grassland might recover from a period of heavy grazing, and how alterations in spring water availability as well a midseason deluge might impact regrowth capacity. Here we found that the experimental alteration in the spring water balance reduced the capacity of this grassland to regrow after simulated grazing by 45% (Fig. 3.4). Further, the addition of a midseason deluge (in a wet year) increased regrowth by 3-fold (comparing A to A + De, Fig. 3.4). Because we did not expect growth to be water limited in this year with above average precipitation, we assessed how the treatments affected soil N availability during this latter half of the growing season (Fig. 3.5). The deluge addition at midseason increased N availability relative to the A treatment suggesting that greater soil water in the latter half of the growing season increased N mineralization, but regrowth potential did not appear to be N limited in the Dr + De treatment. Thus, differences in water availability and the timing of its availability still appear to be the primary mechanism for these ANPP differences, even in a wet year, in this semi-arid grassland. Given that grazing by domestic livestock is the predominant land use of this grassland ecosystem type (Milchunas et al. 1988, Lauenroth and Burke 2008), and this is true of most semi-arid grasslands globally (Stebbins 1981, Milchunas et al. 1989, White et al. 2000), this sensitivity to both early spring precipitation inputs and deluges suggests that management strategies in these grasslands may need to be altered as precipitation regimes change in the future.

3.6 Figures

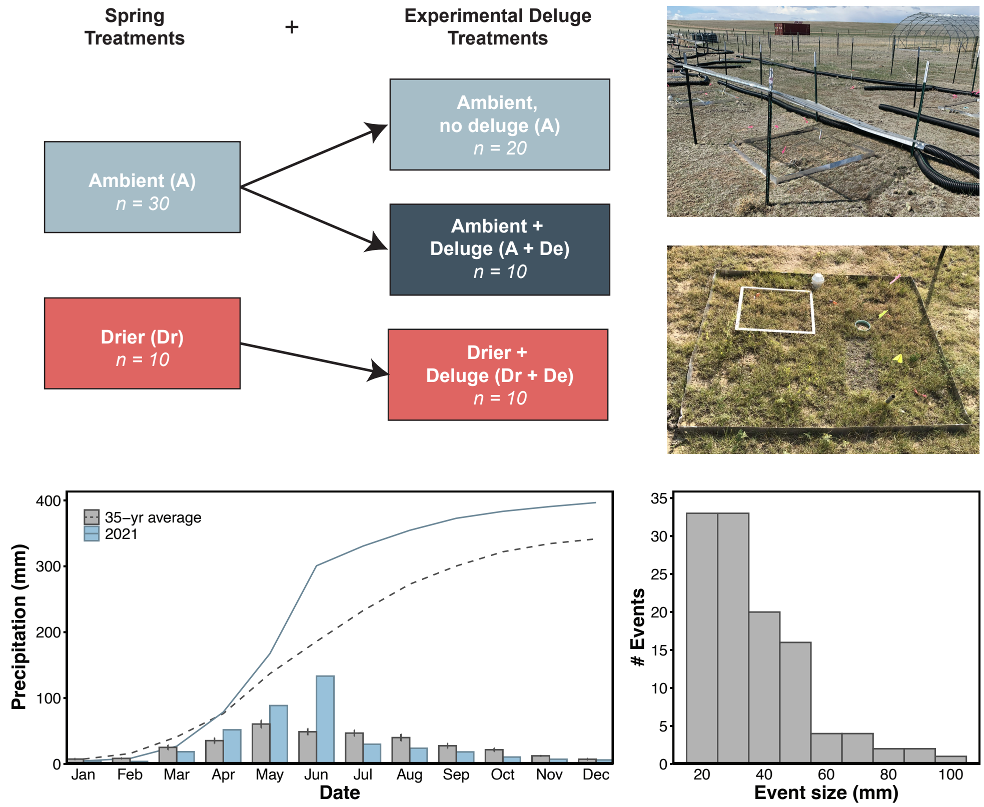

Figure 3.1. Experimental design and site conditions. Treatments were applied in the spring by using full plastic roofs (pictured) to simulate “drier spring” (D) treatment or ambient (no roofs) conditions. The experimental deluge treatment was added over July 15–16, with all drier spring (D) plots and a portion of ambient spring (A) plots received the experimental deluge, compared to the remaining plots with an ambient spring and no deluge treatments. The plot pictured shows measurements for all response variables: the capped PVC tube for soil volumetric water content (Soil$_{VWC}$) from 0-100cm, the open PVC collar for soil respiration (CO_2 efflux, Soil$_{Resp}$), an area clipped for aboveground productivity (ANPP), three pairs of probes to measure soil nutrient availability (purple and orange probes distributed across plot), and an undisturbed 0.25m^2 area (in this case, the bottom left corner of the plot) reserved for canopy greenness (GCC) photos. The combined line/bar graph shows precipitation in 2021 compared to 30-year long term average (LTA) annual precipitation (1990-2020) in Nunn, Colorado, the location of our study site, with bars showing monthly distribution of precipitation in 2021 (blue) compared to monthly LTAs (gray; ± 1 SE) and lines for cumulative annual precipitation. Histogram shows the historical distributions (1990–2024) of large rain events (deluges – defined as any day or consecutive rain days that combined totaled ≥ 20mm total precipitation) during the growing season (April 1 – September 15).

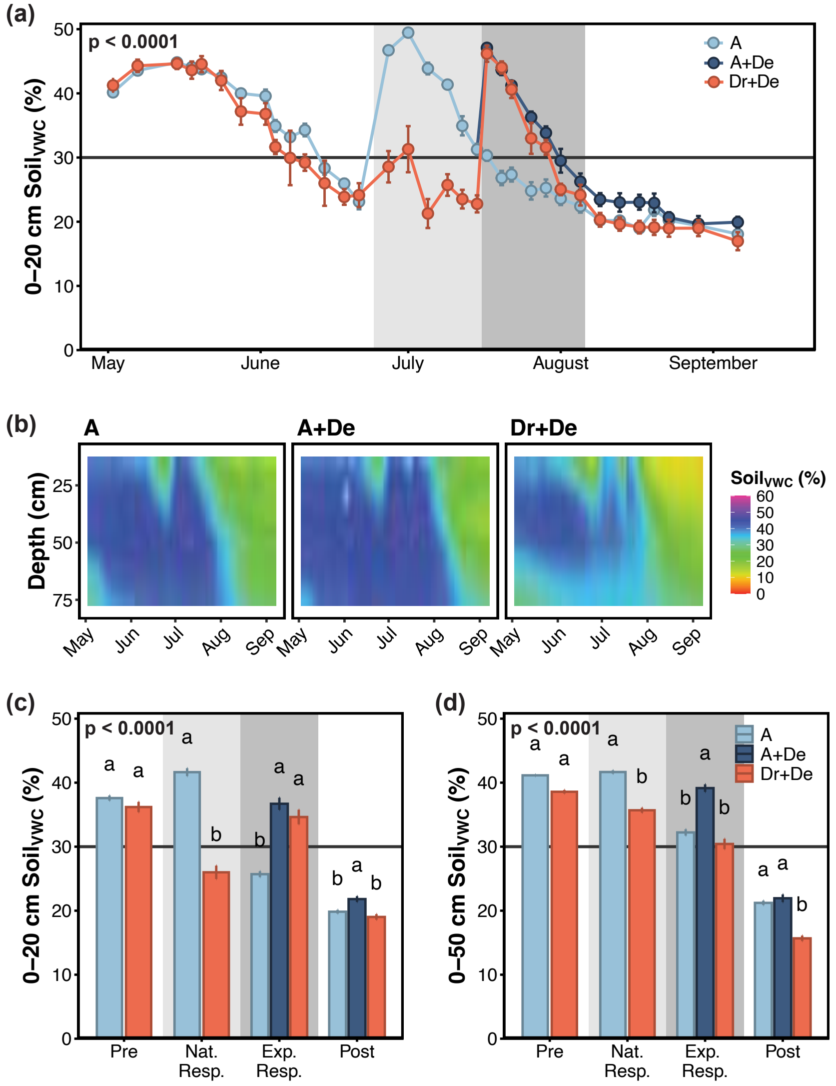

Figure 3.2. (a) Soil volumetric water content (Soil$_{\mathrm{VWC}}$, %) over the course of the growing season at 20 cm. **(b)** Soil moisture interpolated over depth and time for each of the three treatments. **(c-d)** Averaged (± 1 SE) 0-20 cm and 0-50 cm Soil$_{\mathrm{VWC}}$ (from full data shown in a-b) separated by deluge response periods: "Pre" – before natural or experimental deluge, "Nat. Resp." (light gray shading) – between natural and experiment deluges, "Exp. Resp." (dark gray shading) – experimental deluge response period, and "Post" – end of deluge response period through end of growing season. P-values indicate significance of Treatment × Deluge interactive effects (Table A2.2-2.3) and different lowercase letters indicate significant differences between treatments within each deluge response period (see Appendix S1: Fig. S1 for pairwise comparisons including interactions). Ambient treatments (A and A + De) are combined for all dates and response periods prior to the experimental deluge. The horizontal line at Soil$_{\mathrm{VWC}}$ = 30%, a conservative threshold for water limitation in this system (Hoover et al. 2022, Post and Knapp 2021, Saxton and Rawls 2006).

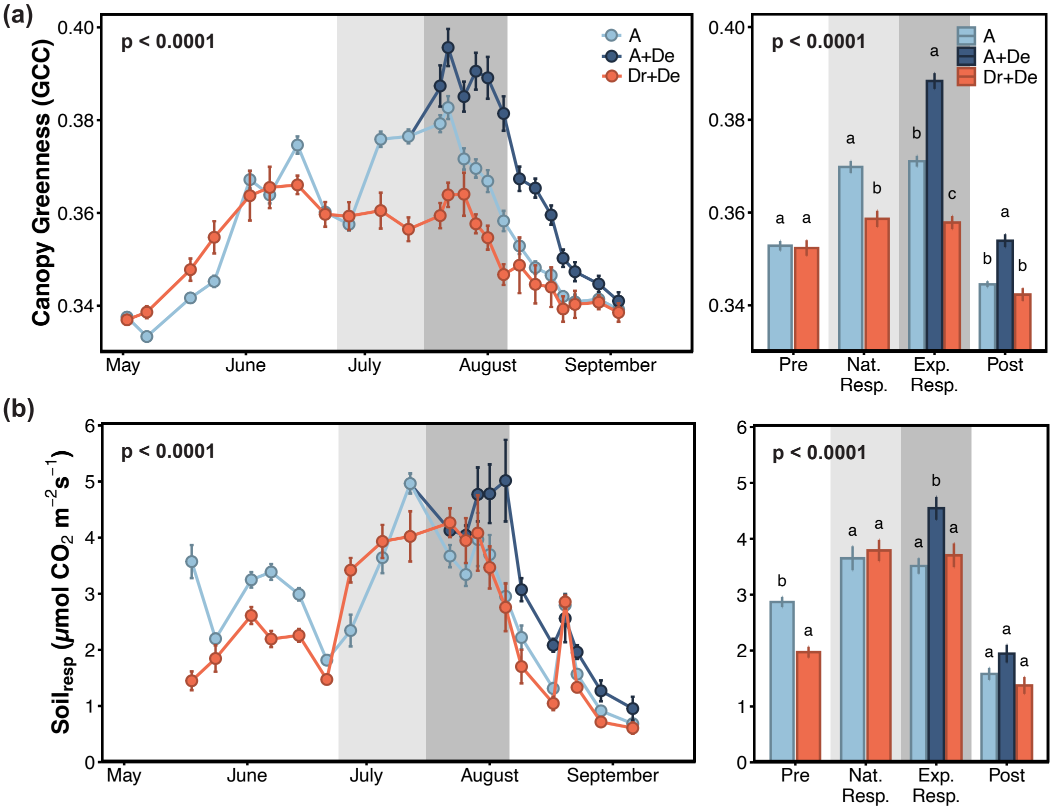

Figure 3.3. Aboveground and belowground responses in **(a)** canopy greenness (greenness chromatic coordinate; GCC) and **(b)** soil respiration (Soil$_{resp}$, μmol CO$_2$ m^{-2} s^{-1}) over the growing season (left line plots) and averaged by deluge periods (right bar plots). Averages bars (mean ± 1 SE) are separated by deluge response periods: "Pre" – before natural or experimental deluge, "Nat. Resp." (light gray shading) – between natural and experiment deluges, "Exp. Resp." (dark gray shading) – experimental deluge response period, and "Post" – end of deluge response period through end of growing season. P-values indicate significance of Treatment × Deluge interactive effects (Table A2.2-2.3) and different lowercase letters indicate significant differences between treatments within each deluge response period. Ambient treatments (A and A + De) are combined for all dates and response periods prior to the experimental deluge. Aboveground responses for GCC are clearer than belowground efflux, which is highly variably throughout the season.

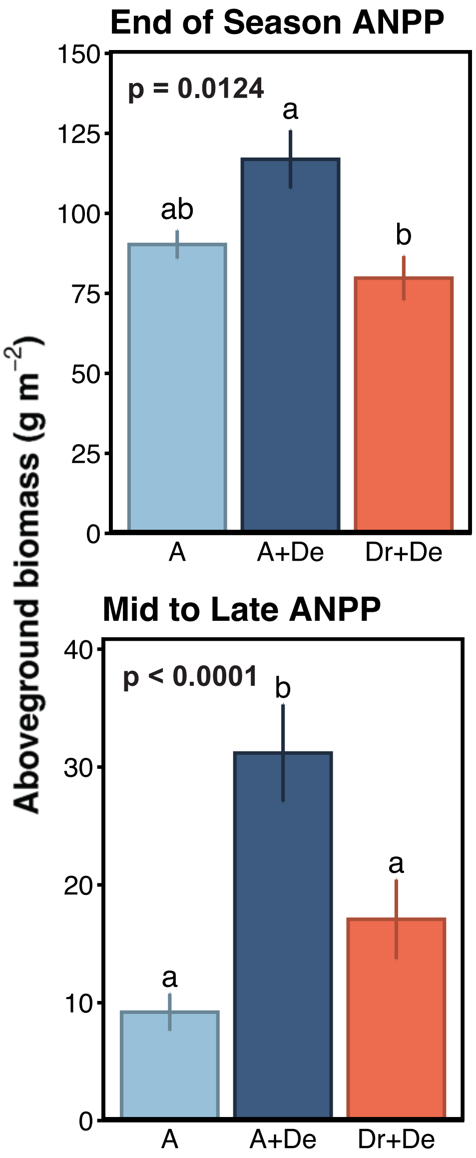

Figure 3.4. End of season aboveground net primary production (ANPP) collected in early September (top), and ANPP regrowth from mid-July to early September ("Mid to Late", bottom). Note differences in magnitudes of each axis. P-values indicate significant main effects of treatment from separate simple linear regressions (Table A2.4) and different letters indicate significant pairwise comparisons. End of season ANPP was significantly lower in Dr + De plots compared to A + De (with A plots falling between and not significantly different from either). Regrowth was significantly higher in the A + De plots relative to the Dr + De plots. Mid-season ANPP (collected in July; not shown) was not different in plots with ambient or drier spring conditions.

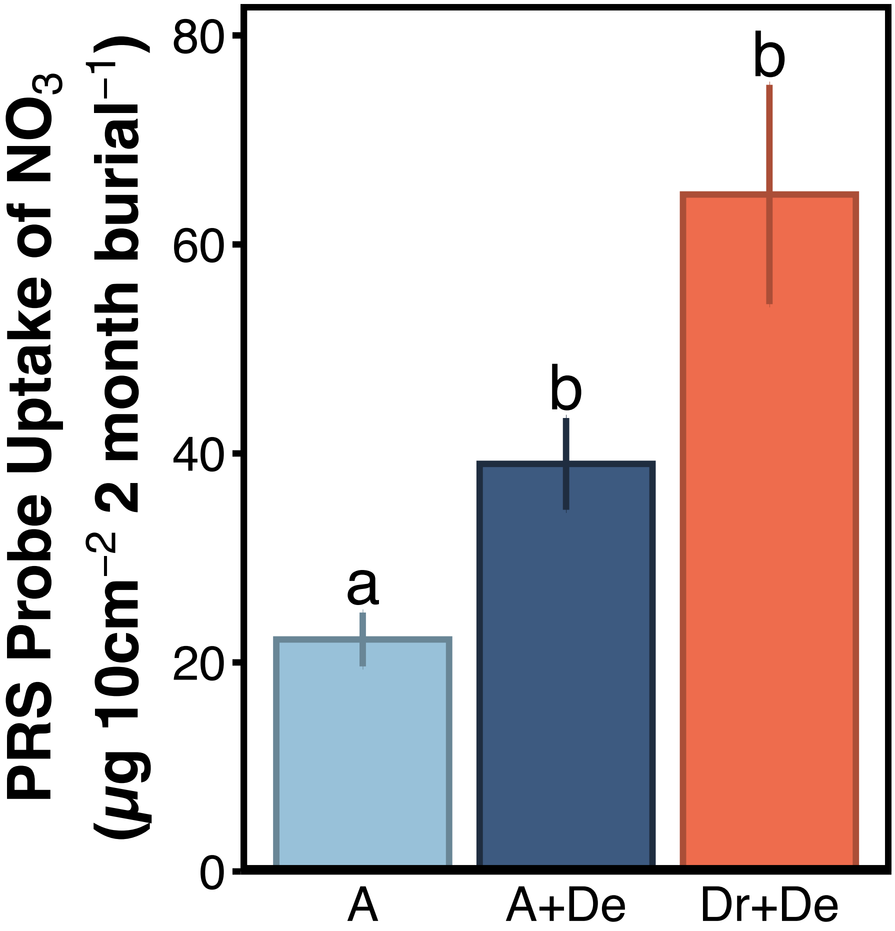

Figure 3.5. Nitrate availability over the 2 months following our experimental deluge addition. The p-value indicates significant main effects of treatment from simple linear regression ANOVA (Table A2.5) and different letters indicate significant pairwise comparisons. Both deluge addition treatments showed increase Nitrate availability, with Dr + De showing the greatest availability, though not significantly different than A + De.

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CHAPTER 4: DO YEARS WITH EXTREME PRECIPITATION ANOMALIES MAGNIFY LEGACY EFFECTS IN ECOSYSTEMS?[3]

4.1 Summary

1. Anthropogenic global change has amplified the hydrological cycle, increasing the frequency and magnitude of extreme precipitation years. Grasslands are particularly sensitive to interannual variations in precipitation, and it is well-documented that the legacy effects of previous year precipitation or production can modify ecosystem functioning in subsequent years. Theory suggests that extreme precipitation years should magnify the impact of antecedent years' precipitation, but this prediction is understudied.
2. We assessed legacies of extreme dry and wet years by adding water in consecutive naturally-occurring extreme drought and average years in northern Colorado's semi-arid shortgrass steppe. Our goal was to assess legacy impacts – alterations in resources and ecosystem structure and function that may carry over from previous years – after extreme precipitation years. Specifically, we 1) paired a naturally-occurring extreme drought in 2022 with a water addition treatment that simulated an average growing season, and then 2) assessed ecosystem responses in these plots in the following year to average or extreme wet precipitation treatments. In addition, we opportunistically quantified the legacy effects of these antecedent extremes during a second natural extreme drought in 2024.
3. We found evidence for both positive and negative legacy effects on key resources and ecosystem function in this grassland. In 2023, soil moisture was reduced early in the growing season after the natural 2022 extreme drought, but the 2023 extreme wet

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[3] Condon KV, Tooley EG, Siggers JA, Sturchio MA, Hajek OL, Knapp AK. Do years with extreme precipitation anomalies magnify legacy effects in ecosystems? Submitted to *Journal of Ecology*.

treatment negated this legacy. Soil N remained *increased* throughout the growing season after extreme drought but also disappeared with extremely high precipitation. Regardless of current precipitation, canopy greenness responded positively to a past extreme drought early in the season, with current conditions dominating later in the season. A positive legacy effect of extreme drought on mid-season ANPP was also evident, but not under extreme wet conditions. Conversely, prior extreme drought reduced soil CO_2 flux only with current precipitation extremes. Finally, the extreme drought in 2024 eliminated most legacy effects.

4. **Synthesis:** We found little evidence that consecutive extreme precipitation years magnified legacy effects. Instead, extreme years more often muted precipitation legacies due to the strong control that current year's precipitation exerts on ecosystem functioning.

4.2 Introduction

Climate extremes are predicted to increase in both frequency and severity, with this dimension of climate change substantially impacting ecosystem structure and functioning (Hoover et al. 2022; Easterling et al. 2000; Grimm et al. 2013; Gulev et al. 2021). While there is ample evidence that increased hydrological extremes are occurring across multiple ecosystems (Huntington 2006; Zeppel et al. 2014; Knapp et al. 2015; Du et al. 2020; Tabari 2020; Chiang et al. 2021, Zhang et al. 2021), the effects of precipitation extremes are not restricted to periods *during* or immediately after extreme events, as some impacts can persist long after the anomaly ends (Sala et al. 2012; Anderegg et al. 2015; Dudney et al. 2017; De Boeck et al. 2018; He et al. 2025).

Grassland ecosystems are particularly sensitive to interannual variations in precipitation and thus respond strongly to precipitation extremes, including extreme drought (Staurt-Haëntjens et al. 2018; Knapp et al. 2024), increased precipitation or shifts in precipitation timing (Parton et al. 2012; Zeppel et al. 2014; Hahn et al. 2021,Hajek and Knapp 2022, 2024; Hajek et al 2024), and heavy rainfall (deluges; Hoover et al. 2022; Post and Knapp 2021). Often, accounting for previous year's conditions (precipitation, productivity, etc.) better explains current-year responses than current conditions alone (Oesterheld et al. 2001; Sala et al. 2012; Dudney et al. 2017; Petrie et al. 2018; Hahn et al. 2021; Vincente-Serrano et al. 2022; Peters and Savoy 2023; Goodman and Felton 2025). The rising frequency of extreme precipitation years may magnify the effects of previous year conditions, but the interaction between current and previous extreme precipitation years (wet or dry) is relatively unexplored. Further, increases in the severity or magnitude of precipitation extremes may also be expected to lead to larger legacy effects after those extremes subside (Sala et al. 2012; Petrie et al. 2018; Felton et al. 2021).

While research evaluating ecosystem recovery post-drought is growing (Vilonen et al. 2022), it is limited compared to our understanding of immediate drought impacts (Knapp et al. 2024). Additionally, although multiple studies emphasize the importance of studying precipitation legacies in general or drought legacies specifically, the legacies of extreme wet years have been less emphasized. Previous studies and theory suggest that either extreme wet or dry antecedent conditions may lead to both positive (greater than expected based on current conditions) and negative (less than expected based on current conditions) legacy effects (Sala et al. 2012; Griffin-Nolan et al. 2018b; Gong et al. 2020; Hahn et al. 2021; Peters and Savoy 2023; Goodman and Felton 2025). For example, positive drought legacies may occur when there is a pulse in N availability upon rewetting due to increased mineralization and decomposition (Birch

1958) or positive legacies of a wet year may occur after increased productivity leads to increased litter and thus higher N availability (Evans and Burke 2013). Negative legacy effects following drought could be due to plant mortality or losses of plants organs that then limits uptake when resources increase. Transitions from wet antecedent conditions to dry are responsible for many negative legacy effects following wet years. Increased leaf area developed during a wet period may leave individual plants more susceptible to water loss during a dry period (Sala et al. 2012), a type of structural overshoot (Zhang et al. 2021). Both drier and wetter antecedent conditions may also cause shifts in species composition, favoring perennial or annual species differently which may lead to increased or decreased grass and forb abundance (Sun et al. 2022; Dudney et al. 2017).

Our goal was to identify and quantify legacy effects – the effects of a drought or extreme wet period that persist after the extreme period has ended (Sala et al. 2012). We manipulated precipitation by adding water during two consecutive growing seasons (a natural extreme drought year followed by an average precipitation year) and continued monitoring into a third, additional, natural extreme drought year. This allowed us to compare (1) interactive effects of antecedent drought or average conditions (2022) potentially expressed during a subsequent year with average or extreme wet conditions (2023), and (2) legacy effects of multiple past extreme years under an extreme drought in 2024.

Our study took place in the semi-arid shortgrass steppe native to northern Colorado. Precipitation–productivity relationships in this grassland have been studied in-depth, including multiple long-term studies assessing the implications of legacies of previous year precipitation (Lauenroth & Sala 1992; Sala et al. 2012; Petrie et al. 2018; Hoover et al. 2021) and production (Oesterheld et al. 2001; Hoover et al. 2021; Goodman and Felton 2025) and several shorter-term opportunistic studies of drought or experimental manipulations (Griffin-Nolan et al. 2018b; Hajek and Knapp 2024; Condon et al. 2025). Based on these studies, we expected to see overall negative legacy effects following drought, where ecosystem functioning (aboveground productivity, canopy greenness, and soil respiration) would remain reduced in previously-droughted plots regardless of current-year conditions. We also expected that the negative effects of a current-year drought would be less impactful when preceded by an extreme wet year (Oesterheld et al. 2001; Petrie et al. 2018; Peters and Savoy 2023). We focused on responses in soil moisture and soil nitrogen, both potential mechanisms of precipitation legacy effects; soil respiration, a major contributor to carbon cycling in this system; and aboveground productivity and canopy greenness, both of which can indicate the availability (amount and timing) of forage for native and domestic grazers.

4.3 Methods

4.3.1 Site Descriptions

The study took place at the Central Plains Experimental Range (CPER) in northern Colorado (Weld County, Colorado) from 2022 through 2024. The CPER is a US Department of Agriculture – Agricultural Research Service (USDA-ARS) site dominated by semi-arid shortgrass steppe, with blue gramma (*Bouteloua gracilis*) and buffalograss (*Bouteloua dactyloides*) the co-dominant native C_4 grasses. Mean annual precipitation (MAP) in the area is 340 mm with >70% (246 mm) of that precipitation occurring during the growing season, defined here as April 1 – Sept. 15 (Table 4.1). Interannual variability in net primary productivity (NPP) in this grassland is generally strongly correlated with interannual variability in precipitation (Noy-Meir 1973; Sala et al. 1992). In our study area, average aboveground NPP (ANPP) was 72.9 ± 11.2 g m^{-2} based on 2012-2024 ambient ANPP averages, though annual ANPP across the

CPER can range from ~10-200 g m^{-2} (Table 4.1; Hoover et al. 2021). Although productivity in semi-arid ecosystems is low, the high sensitivity to precipitation leads to high variability in year-to-year productivity and contributes to interannual variability in the carbon cycle at the global scale (Poulter et al. 2014; Ahlström et al. 2015). Both native and domestic grazers have historically used the shortgrass steppe for forage (Laurenroth and Burke 2008), though grazing was excluding for nearly 8 years prior to and throughout the project period.

We used a combination of precipitation data from the USDA site data and data accessible through the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information online Climate Data Tools (https://www.ncdc.noaa.gov/cdo-web/datatools) from the nearest NOAA stations (Menne et al. 2012a,b) to assess long-term average (LTA) precipitation data and create daily precipitation records during the non-growing season. Ambient precipitation during the growing season was monitored using USDA site data when available and a nearby Soil Climate Analysis Network (SCAN; ID: SC2197). Daily and monthly LTA temperature records were assembled from PRISM data (PRISM Climate Group 2024, https://prism.oregonstate.edu).

In 2022, MAP and growing season precipitation (GSP) were 25 and 39% below the 30-year long-term precipitation averages, which, combined with higher-than-average growing season air temperatures, led to a 68% reduction in end-of-season ANPP (Table 4.1; Figure A3.1). Thus, from an ecosystem function perspective, this was an extreme drought year (Hoover et al. 2021). Precipitation in 2023 was slightly above-average – ~9-16% above LTA MAP and GSP, respectively – but ANPP did not differ as substantially from the long-term average (Table 4.1; Figure A3.1). Another extreme drought year occurred in 2024 with precipitation reduced by 27-30% and ANPP by 72% (Table 4.1; Figure A3.1). It is notable that the greatest divergences in precipitation from LTA precipitation patterns occurred during June in 2022 and 2023 (Figure 4.1), and spring precipitation has been shown to be a disproportionate driver of ecosystem functions in this grassland (Parton et al. 2012; Hoover et al. 2021).

In sum, based on precipitation amounts and patterns, air temperatures, and end-of-season ANPP, we considered both 2022 and 2024 ambient conditions as extreme drought years, with 2023 as an ambient average year (Figure A3.1). On this template of extreme droughts separated by an average year, we added water to experimentally manipulate growing season precipitation in 2022 and 2023 – which offset the drought in 2022 and imposed an extreme wet and high productivity year in 2023. This allowed us to compare response to and legacy effects of multiple combinations of extreme years in 2022 through 2024.

4.3.2 Experimental Design and Treatments

We used a fully randomized 2 x 2 factorial design with the same 40 independent, 1 m^2 plots used across all years. In 2022, we randomly assigned 20 plots to ambient treatment (no manipulation but a natural extreme drought) and the other half were watered throughout the growing season, which, combined with the dry and particularly hot ambient conditions (Table 4.1), brought productivity up to average levels. In 2023, we again randomly assigned 20 plots to the watering treatment, grouped within the previous treatments of 2022 to achieve n = 10 plots of each combination of drought (D) or average (Av) conditions in 2022 with ambient average (Av) or extreme wet (W) treatments in 2023. Our experiment was initially planned only for two years, but in 2024 a natural extreme drought allowed us to further assess legacy effects following the previous two treatment years (D→Av, D→W, Av→Av, or Av→W) for a subset of response variables.

During each treatment year, plots assigned to the water addition treatments were each bordered with ~ 15 cm aluminum flashing buried to ~ 10 cm depths with a portion left above ground to prevent overland flow during watering. Including plot borders, each plot was 1.5 x 1.5 m and only the inner 1 m^2 area was used for measuring response variables. Flashing was installed only in the plots assigned to the watering treatments at the beginning of each growing season (late April – early May), then removed at the end of the growing season to avoid creating areas that would accumulate snowfall over the winter.

We used potable water for water-addition treatments, with nitrate and other nutrient levels below drinking-water standards. Commercial garden wands equipped with a low flow digital meter (Great Plains Industries, Wichita, Kansas, USA) were used to add water to the plots. We added water at a rate that minimized water pooling at the soil surface (and vulnerable to evaporation; Parton et al. 1981). Typically, 6-18 mm of simulated rainfall was added in a single day, with larger additions split over multiple rounds of watering to allow time for complete infiltration into the soil. During dry periods, water was added more frequently, with fewer additions (as needed to supplement weekly ambient rainfall) during wet periods. Initially, our goal was to simulate similar extreme wet growing season treatments during 2022 and 2023, but despite watering to similar growing season totals in both years (~400 mm), the substantially higher air temperatures and vapor pressure deficits in 2022 resulted in a functionally average year based on productivity responses.

4.3.3 Measured Responses

We measured volumetric water content (Soil_{VWC}) at 20 cm depth, soil respiration ($\text{Soil}_{\text{Resp}}$) and soil temperature (at 10 cm depth), and canopy greenness continuously throughout each growing season. ANPP was also measured by harvesting mid- and end-of-season biomass as well as the regrowth from harvest plots from mid-to-late season in 2023. In 2022 and 2024, we only harvested end-of-season biomass, in part because the extreme drought conditions during both of these years resulted in extremely low mid-season biomass with little or no distinguishable current-year plant growth to collect. Soil nutrient availability was measured in 2023 over two 7-week periods: early- to mid-growing season (May 18, 2023, to July 6, 2023) and mid- to late-growing season (July 6, 2023, to August 24, 2023). When any data measurements and treatment water additions fell on the same day, all measurements were taken prior to watering to avoid short-term immediate effects from the simulated rainfall.

Continuous response variables (20 cm Soil_{VWC}, $\text{Soil}_{\text{Resp}}$, and canopy greenness) were measured 1-2x weekly during the 2022-2023 growing seasons and biweekly during 2024 (for 20 cm Soil_{VWC} and canopy greenness only). We used the same ~7-weeks of the soil nutrient probe installations (May 18–July 6, 2023 and July 6–August 24, 2023) to identify trends across early (prior to July 6) and late (after July 6) growing season periods for each of these responses in all years.

Soil_{VWC} was measured with Campbell Scientific Hydrosense II handheld time-domain reflectometry probes in a dedicated area of each plot away from plot edges. In a subsample of plots (n = 10 per the two treatments in 2022 and n = 5 per the four treatments in 2023), we installed soil respiration collars in an area of mostly bare soil (removing small amounts of standing plant biomass as needed). We used a LI-COR 6400XT portable photosynthesis system equipped with a soil CO_2 flux chamber which fit over the collars of each plot to measure $\text{Soil}_{\text{Resp}}$, or CO_2 efflux, a combination of root and microbial respiration. These measurements were made between 9 am and 1 pm on each measurement day with soil temperature measured simultaneously at 10 cm depth outside of the collar. We evaluated changes in canopy greenness using repeat photographs taken from directly above a dedicated 0.25 m^2 undisturbed area of each plot. Photos were cropped to the inner boundary of the 0.25 m^2 quadrat using Adobe Photoshop (https://www.adobe.com/). Cropped images were then analyzed with the EBImage package (Pau et al. 2010) in R version 4.4.1 (R Core Team 2024), where each pixel in the image is assessed for the ratio of greenness relative to the total brightness of the photo. The average of all pixels is taken to obtain a mean green chromatic coordinate (GCC) for the image.

Aboveground biomass was measured two times during the 2023 growing season and once during the extreme drought years, 2022 and 2024, as an estimate of ANPP (Fahey and Knapp 2007). ANPP was estimated by clipping all aboveground plant material in a 0.2 x 0.5 m^2 subplot of each plot, once in early September each year to estimate total biomass and additionally in 2023 at the midseason. Additionally, we evaluated regrowth in 2023 by harvesting midseason ANPP initially in July and the same subplots harvested again in September to measure the biomass that had grown back in the area. Biomass was sorted into plant functional groups (C_3 grasses, C_4 grasses, annual grasses, and forbs) in the field then sorted again to remove dead plant material from previous years in the lab before being dried at 60 ºC for 2 days and weighed to the nearest 0.01 g. Soil nutrient availability was measured with Western Ag Plant Root Simulator (PRS®) probes that use ion exchange resin membranes to attract and absorb anions or cations from soils. In each plot, we installed three pairs of probes (with each pair including one anion and one cation probe) just below soil surfaces in three areas distributed across the plot for 7 weeks at a time (May 18–July 6 and July 6–August 24).

4.3.4 Data Analysis

All analyses were performed using R version 4.4.1 (R Core Team 2024) with significance assessed at $\alpha = 0.05$. For each of our continuous variables ($Soil_{VWC}$, $Soil_{Resp}$, and GCC), we evaluated effects at three different time scales: differences in daily measurements during the entire growing season, the differences between treatments averaged across the growing season, and average treatment differences for early and late growing season periods. Aboveground net primary productivity (ANPP) and soil N availability were analyzed individually for each time they were measured (2022-2024 for ANPP and 2023 early and late season for soil N).

Each of the continuous variables were analyzed first on the daily scale separately for each year using mixed-effects linear models with $\mathrm{Soil}_{\mathrm{VWC}}$, $\mathrm{Soil}_{\mathrm{Resp}}$, or GCC as the response variable and fixed effects for the sampling date, treatment in 2022 (for all years) and 2023 (for 2023 and 2024 responses only) and all interaction effects. Plot ID's were included as a random effect in each model to account for repeated measures of the same plots over time. We used the full models including all daily measurements to identify outliers using the outlierTest function in the car package (Fox and Weisberg 2019). Outliers that were identified as significant were checked and dropped from the data used for the daily models and all further analysis, but only if measures seemed ecologically unreasonable *(e.g.,* clear equipment or recording errors). We then used the "step" function of the lmerTest package (Bates et al. 2015) to reduce each model's fixed effects and confirmed preferred models by comparing the full and reduced versions using the anova function in the car package (Fox and Weisberg 2019). Emmeans pairwise comparisons (with Tukey or Bonferroni correction; Lenth 2024) were used to check treatment differences for significant interactions or fixed effects.

To assess average differences across the entire growing season or within the early vs. late growing season periods each year, we averaged the daily measurements to one value per plot for the season or each period. To compare responses averaged across the entire growing season, we used t-tests to compare the two treatments in 2022 and used linear regressions and ANOVAs to compare the four treatments in 2023-2024. Separate t-tests or linear regressions were used for each response variable measured each year: $Soil_{VWC}$, $Soil_{Resp}$, GCC, and soil nutrient availability (in 2023 only). Each linear regression had average $Soil_{VWC}$, $Soil_{Resp}$, GCC, or nutrient availability as the response variable and fixed effects for the 2022 and 2023 treatments. When comparing growing season periods (early vs. late), we included an additional fixed effect for the period and a random effect for Plot ID to account for repeated measures. Analyses for ANPP was similar but used only simple linear regressions, fit separately for each collection time (mid- or end-season) of each year. Our primary focus was on quantifying legacy effects, so we followed each of the 2023 regressions with emmeans pairwise comparisons (Lenth 2024) to assess for differences driven by 2022 treatment effects (D or Av) within each 2023 treatment (Av or W). Similarly, we expected more recent years to have the strongest effects on responses during the 2024 extreme drought, so we used the same method to compare main effects of 2022 or 2023 treatments on 2024 responses, followed with pairwise comparisons of 2022 effects within each 2023 treatment.

4.4 Results

4.4.1 Precipitation Addition

Ambient growing season precipitation, and thus $Soil_{VWC}$, was lowest during the extreme drought years, 2022 and 2024, with total GSP = 148.80 and 169.42 mm, respectively. In 2023, ambient precipitation was slightly above average (283.21 mm compared to 242.41 mm LTA GSP). As expected, precipitation manipulations in 2022 led to significant increases in $Soil_{VWC}$ (D vs. A $p < 0.0001$; Figure 4.2a) compared to ambient extreme drought conditions – indicating the effectiveness of our water additions. The watering treatments in 2023 resulted in considerably higher $Soil_{VWC}$ than in 2022, likely due the hotter, drier conditions during the 2022 drought

(Table 4.1). But from an ecosystem function perspective, the watering treatment in 2022 led to an average year in ANPP (76.8-79.9 g m^{-2}; Figure 4.4).

As a result of our hydrological manipulations during the first year, there were significant decreases due to the ambient extreme drought (D) conditions compared to the average year (Av) treatment in all responses: Soil_{VWC} (Figure 4.2 and A3.2; Table A3.1) $\text{Soil}_{\text{Resp}}$ (Figure A3.3, Table A3.1), canopy greenness (GCC; Figure 4.3d; Table A3.1) and mid- and late-season aboveground net primary productivity (ANPP; Figure 4.4a and Table A3.4). In 2023, Soil_{VWC} was generally higher for the simulated extreme wet current-year plots (W; Figure A3.2), but legacy effects of the 2022 treatments were evident for all plots in 2023 – with stronger evidence of positive Soil_{VWC} legacies early in the growing season for Av→Av treatments ($p = 0.0495$ early vs. $p = 0.1086$ late; Figure 4.2b) and later in the growing season for the Av→W treatments ($p = 0.0941$ early vs. $p = 0.0033$ late; Figure 4.2b). During the extreme drought in 2024, there was no evidence of Soil_{VWC} legacies from any combination of the previous two years. Soil_{VWC} remained low for the majority of the 2024 growing season and did not differ when separated by previous treatments (Figure 4.2c and A3.2).

For most measures of ecosystem responses, differences in current-year treatments were significant, especially when averaged across the entire growing season (Table A3.1). However, there was some evidence of legacy effects of 2022 treatments during 2023, especially for comparisons including all dates or within early-to-mid and mid-to-late growing season periods (Tables A3.2-A3.3). During the extreme drought in 2024, legacy effects from any combination of antecedent conditions were not common.

4.4.2 Legacies in Aboveground Responses

In 2023, there was no evidence of legacy effects in canopy greenness (GCC) averaged across the growing season (Table A3.1), but for all plots droughted in 2022 (D→Av and D→W), GCC was significantly increased (positive legacy effect) during the early growing season (Figure 4.3b & e). The current conditions of 2023 dominated greenness during the mid-to-late growing season period, with generally higher GCC, or later senescence, under current extreme wet conditions compared to average conditions (Figure 4.3b & e). During the 2024 extreme drought, GCC was much lower and stable over the entire season, with no legacy effects (Figure 4.3c & f). ANPP responses were similar to GCC responses. Like GCC, ANPP was increased after the 2022 drought at mid-season, though only for D→ Av, not D→W (*i.e.,* drought followed by extreme wet did not show the drought legacy; Figure 4.4b). This contrasted with GCC, where a positive drought legacy effect was evident for both treatments during the early to mid-season period (Figure 4.3e). By end-of-season in 2023, there was no evidence of previous-year effects for either current-year treatment.

ANPP responses were similar to GCC responses. Like GCC, ANPP was increased after the 2022 drought at mid-season, though only for D→ Av, not D→W (*i.e.,* drought followed by extreme wet did not show the drought legacy; Figure 4.4b). This contrasted with GCC, where a positive drought legacy effect was evident for both treatments during the early to mid-season period (Figure 4.3e). By end-of-season in 2023, there was no evidence of previous-year effects for either current-year treatment.

In 2024, both GCC (across the growing season) and end-of-season ANPP showed substantial reductions in response to the natural extreme drought compared to the previous year. While there was no evidence of legacy effects in GCC, there was a greater reduction in 2024 end-of-season ANPP for the driest combination of years: extreme drought in 2022, average in

2023 and extreme drought in 2024 (D→Av→D; Figure 4.4c). However, in the context of the already-reduced ANPP from the extreme drought, this additional reduction was relatively minor (~10 g m^{-2}).

4.4.3 Legacies in Belowground Responses

The greatest evidence for legacy effects on $Soil_{Resp}$ was during the mid-to-late growing season period in 2023, where $Soil_{Resp}$ in all previously-droughted plots was reduced compared to those with the average 2022 treatment (D→Av and D→W; Figure 4.5a). The largest late-season negative drought legacy was evident under the current extreme wet treatment (D→W; $p = 0.0169$; Figure 4.5a), though the average current treatment (D→Av) was also reduced considerably ($p = 0.0810$; Figure 4.5a). $Soil_{Resp}$ was not measured in 2024, though we would expect minimal differences due to antecedent conditions given the extremely low soil moisture with the extreme drought.

Nutrient availability in soils was measured as an additional potential legacy, or mechanism for the changes seen in 2023, assessed for early and late growing season periods with cation/anion exchange probes. Although the probes measured a variety of nutrients, we focus primarily on Nitrogen (N) availability as, after water limitation, the availability of N is a well-known limiting factor of grassland productivity (LaBauer and Treseder 2008; Fay et al. 2015). Ammonium nitrogen (NH_4-N) measures fell below method detection limits for the probes for nearly all plots, so we excluded this measure from analysis, though this may still be an important source of N for plants in the system. Nitrate nitrogen (NO_3-N) availability was increased over the entire growing season after an antecedent drought, but only when followed by the average 2023 conditions (D→Av vs. Av→Av; Figure 4.5b orange bars). NO_3-N availability did not differ based on antecedent conditions under the extreme wet treatment (D→W vs. Av→W; Figure 4.5b blue bars).

4.5 Discussion

Understanding the consequences of changes in precipitation patterns through an increased frequency of extreme dry and wet years is particularly important in semi-arid and arid systems. These systems are especially sensitive to changes in precipitation regimes (Noy-Meir 1973; Sala et al. 1992; Staurt-Haëntjens et al. 2018; Hoover et al. 2021). Despite their comparatively low total productivity, arid and semi-arid ecosystems contribute significantly to the global carbon cycle (Poulter et al. 2014), in addition to providing many other ecosystem services (Bengtsson et al. 2019). Some prior studies have suggested potential buffering effects of oscillating extreme years (*e.g.,* less negative responses to drought with an antecedent wet year, less positive responses to a wet year limited by a previous drought; Oesterheld et al. 2001; Yahdijan and Sala 2006). Others have reported amplifying effects of repeated extremes (*e.g.,* greater negative effects of multiple drought or wet years over time) – where structural changes in ecosystems may be a greater driver of legacy effects than soil moisture carry-over, which may be limited in this system (Oesterheld et al. 2001; Reichmann et al. 2013; Hooever et al. 2021; Parton et al. 1981; Paruelo et al. 1999). Here, we took advantage of natural extreme drought years (in 2022 and 2024) in combination with an experimentally manipulated extreme wet year (in 2023) to further assess how extreme hydrological years interact.

Contrary to our expectations, there was minimal evidence of strong, consistent legacy effects from either extreme drought or wet years. Rather, we found that evidence for legacy effects differs substantially for different ecosystem responses and may only be evident during portions of the growing season. For example, the extreme drought in 2022 seemed to affect

$Soil_{VWC}$ mostly early in the growing season during the average 2023 year (early D→Av), but later in the season during the extreme wet year (late D→W; Figure 4.2). Differences in $Soil_{Resp}$ were also significant for the late-season extreme wet year (late D→W), as we would expect from the $Soil_{VWC}$ differences, but did not differ for early D→Av, despite significant $Soil_{VWC}$ differences also existing then (Figures 4.2 and 4.5). In contrast, we measured legacy effects of drought in both treatment's GCC in 2023, but only for the earlier portion of the growing season. GCC responses by the end of the season were dominated by the current-year conditions. ANPP responded similarly to GCC, with positive drought legacy effects mid-season, but only under the ambient average 2023 treatment (D→Av). Increased N availability could theoretically explain early-season positive GCC responses, especially for the significant increases during the average year treatment following drought (D→Av). But we only observed a slight and non-significant increase in N availability under the watering treatment (D→W). Early-season increases in N availability suggest that a pulse of N was released as decomposition and mineralization in soils increases after rewetting of soils following a dry period (Birch 1958). The lack of differences in N availability in 2023 under the extreme wet (W) treatment most likely reflects increased plant uptake over the growing season, because $Soil_{VWC}$ in 2023 was consistently >30% (a conservative threshold for water limitation of ecosystem processes in this grassland; Hoover et al. 2022; Post and Knapp 2021; Saxton and Rawls 2006). However, even the ambient (Av) treatment remained >20% $Soil_{VWC}$, which would be considered typical for a year with normal precipitation (Post and Knapp 2021). Thus, the continued increase in N availability after drought even into the late season is not fully explained by $Soil_{VWC}$ limitation and does not seem to be the primary mechanism to explain legacy effects across ecosystem responses.

It is important to recognize that legacy effects were often evident when assessing daily measurements and when separated into different periods during the growing season. These tended to be “hidden” when data were aggregated to annual values. For example, early season increases in GCC from previous drought were muted when assessed over the whole growing season since later in the season the dynamics switched, and current conditions dominated (Figure 4.3). Compensatory effects like this have also been identified during the severe drought in the United States in 2012 (Wolf et al. 2016), and other studies also emphasize the importance of temporal scales and seasonality when identifying legacy effects (Smith et al. 2009; Griffin-Nolan et al. 2018a; Petrie et al. 2018; Wen et al. 2025).

The responses during the extreme drought year in 2024 further support the dominance of current-year extremes over legacy effects of antecedent extremes. Soil_{VWC} in 2024 was low, and while the previous wet year showed slightly increased Soil_{VWC} very early in 2024 (Figure A3.2; Table A3.3), this effect did not persist and was only evident in the daily data. GCC similarly showed substantial reductions in 2024 overall, and was consistently low, with no indications of green-up or senescence (Figure 4.3c & f). There was a significant reduction in end-of-season ANPP for the driest combination of years that would be indicative of a *negative* legacy effect (Figure 4.4c). However, since all ANPP in 2024 was reduced so significantly (>70% reduction compared to the long-term average), the additional reduction from the negative legacy would likely have little ecological significance. Previous studies and theory also suggest the importance of cumulative effects of multi-year extremes that follow the same direction (*i.e.,* successions of multiple drought years or multiple extreme wet years) in semi-arid and dryland ecosystems (Felton et al. 2021; Poulter et al. 2014, Ohlert et al. 2025), but the underlying ambient conditions of our experimental years did not allow for such comparisons. The positive drought legacy on

2023 ANPP at mid-season and early greenness does suggest that legacy effects may be more relevant when average seasons follow extremes, rather than an extreme in the opposite direction. But future climate scenarios suggest that extreme years will occur at unprecedented frequencies and magnitudes (Seneviratne et al. 2021), so it is also pressing to understand the interactions between multiple extreme years.

4.6 Conclusions

Contrary to the expectation that hydrologically extreme years (wet, dry) may interact in ways that increase legacy effects from prior years, it appears that during extreme years, legacy effects may be mostly overridden by responses to the current extremes – even if the previous-year extremes were equally or more severe than current conditions. Under future climate scenarios, increases in extreme years are expected (Gulev et al. 2021; Seneviratne et al. 2021). As future climate extremes persist, it is increasingly important to understand how ecosystems will respond to these extremes – not just during the extremes, but potentially for long periods of time after an extreme period ends. However, our results here suggest that extremes, especially in opposite directions, have the capability to mute legacy effects, highlighting the importance of the temporal sequence of extreme years for legacy impacts.

4.6 Tables

Table 4.1. Precipitation, temperature, and aboveground net primary productivity (ANPP) for experimental years (2022-2024) and long-term averages (LTA). The growing season was defined as April 1–September 15 for each year for our climate variables, and LTA precipitation and temperatures are 35-year averages (1990-2024, ± 1 SE). The ANPP LTA is based on the 13-year average (± 1 SE) ambient ANPP from our experimental plots (2022-2024) and from experiments in the immediate surrounding area (2012-2021). For the purposes of our study, 2022 and 2024 were considered natural drought years (note the low ANPP values) whereas 2023 was considered an average year.

	Precipitation (mm)		Average Daily Temperature (ºC)		ANPP
	Annual	Growing season	Annual	Growing season	($g\ m^{-2}$)
2022	255.14	148.80	8.69 ± 3.21	20.1 ± 2.45	23.3 ± 2.6
2023	367.25	283.21	8.79 ± 2.89	19.1 ± 1.77	84.5 ± 9.3
2024	246.32	169.42	10.2 ± 2.73	19.7 ± 2.31	20.3 ± 1.9
LTA	338.38 ± 10.85	242.41 ± 10.55	9.18 ± 0.11	19.3 ± 0.13	72.0 ± 11.2

4.7 Figures

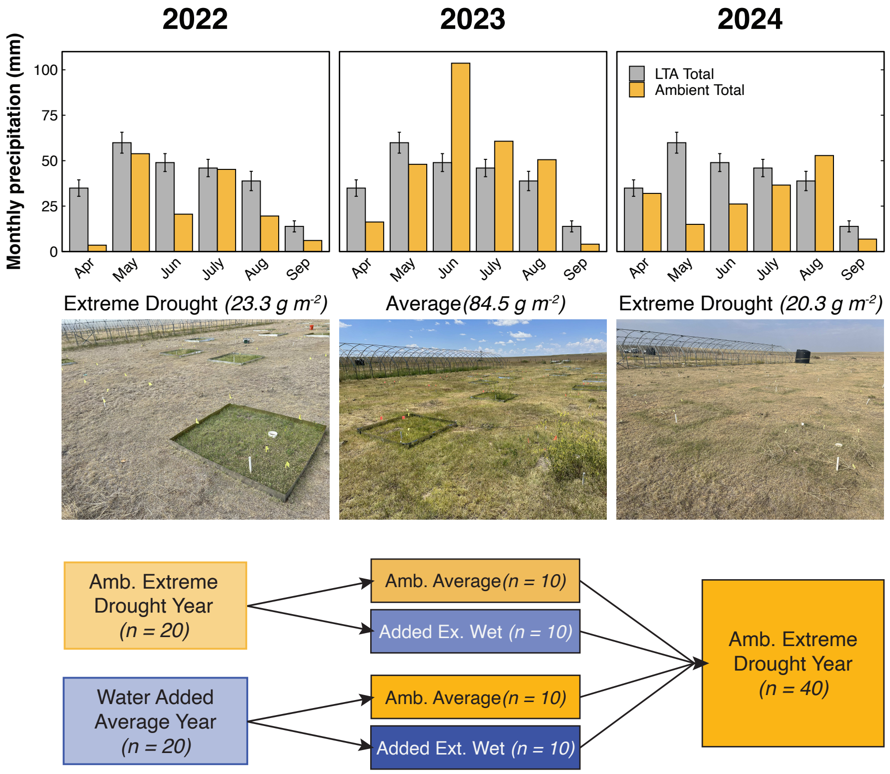


Figure 4.1. Ambient conditions and treatment assignments during the three experiment years. Bars show monthly ambient precipitation from April 1–September 15 for each year (orange) compared to long-term (35-year; 1990-2024) average monthly precipitation (gray bars; long-term mean ± 1 SE). Photos of experimental plots show ambient aboveground net primary productivity (ANPP) in mid-July each year. Water addition plots (in 2022-2023) are surrounded by aluminum flashing boarders during the growing season only. The same (n = 40) plots were assigned to the ambient (no treatment) natural drought or average (with watering) treatment in 2022 and to ambient average or simulated extreme wet treatments in 2023. All plots were monitored under the same in 2024, a second natural extreme drought, and comparisons between plots with different histories used to identify continued legacies effects in this year.

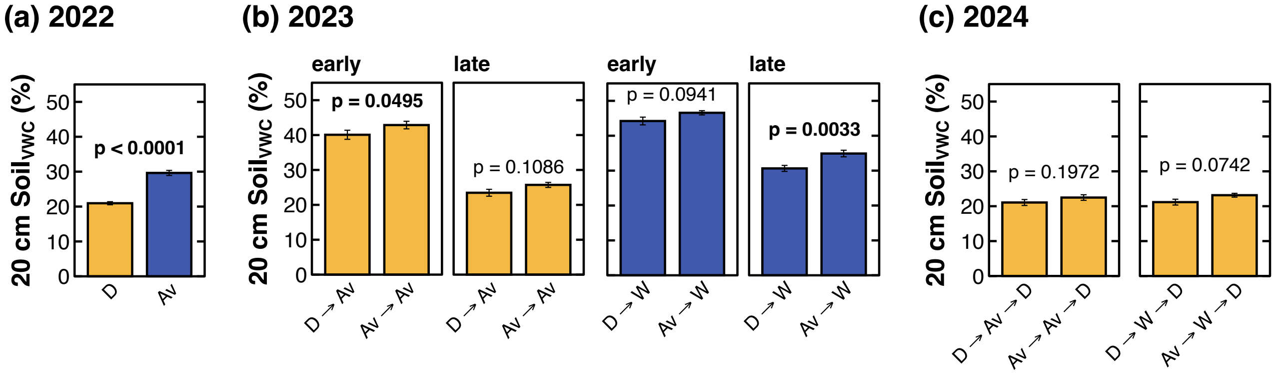


Figure 4.2. Soil$_{VWC}$ at 20 cm depth averaged across the entire growing season for 2022 (a) and 2024 (c) and split for the early-to-mid and mid-to-late growing season periods in 2023 (b). Labels on x-axes correspond to conditions each year (D = extreme drought, Av = average, and W = extreme wet) and colors correspond to current conditions (wetter or drier each year). Precipitation manipulations were imposed from 2022–2023 by adding water, and legacy effects quantified both within the 2023 treatments (ambient average or experimental extreme wet) and from the previous two years during the 2024 natural extreme drought.

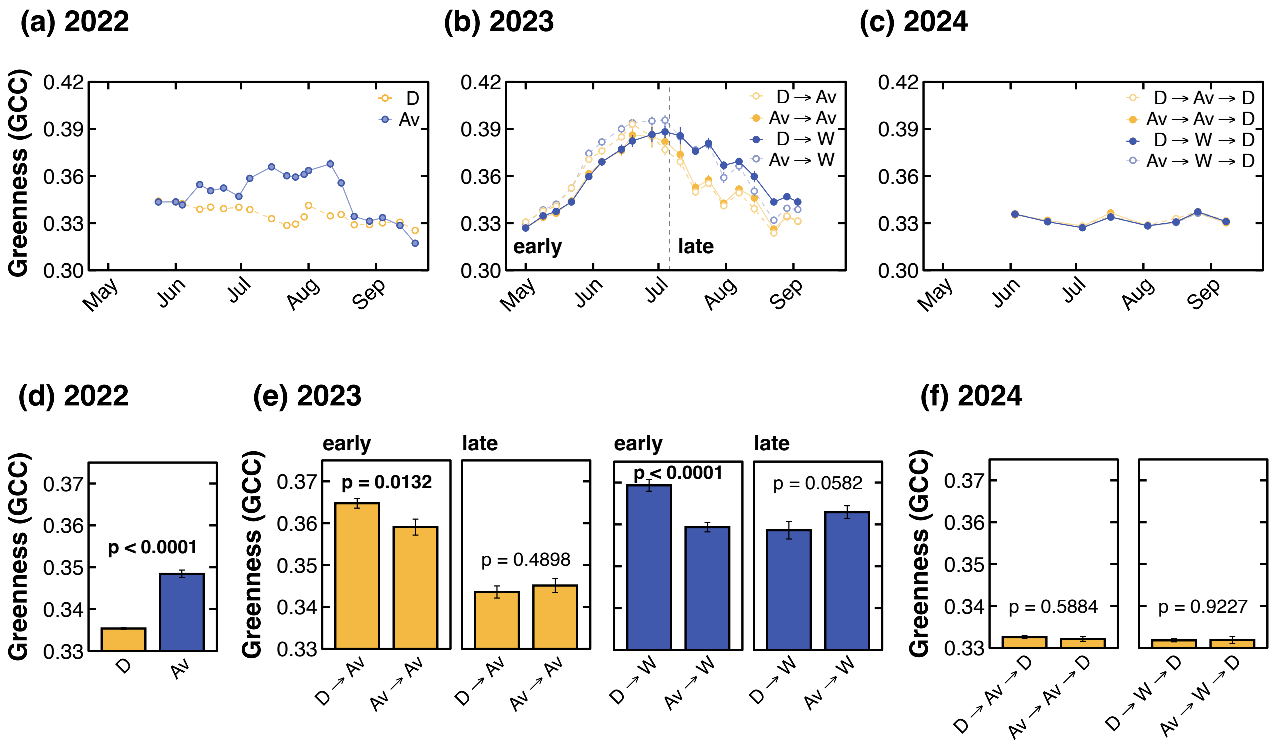


Figure 4.3. Daily measurements of canopy greenness (GCC treatment mean ± 1 SE; a–c) averaged across the entire growing season for 2022 (d) or split for the early-to-mid and mid-to-late growing season periods in 2023–2024 (e-f). Labels with arrows in the legends and x-axes correspond to conditions each year (D = extreme drought, Av = average, and W = extreme wet) and colors correspond to current conditions (wetter or drier each year). Precipitation manipulations were imposed from 2022–2023 by adding water, and legacy effects quantified both within the 2023 treatments (ambient average or experimental extreme wet) and from the previous two years during the 2024 natural extreme drought.

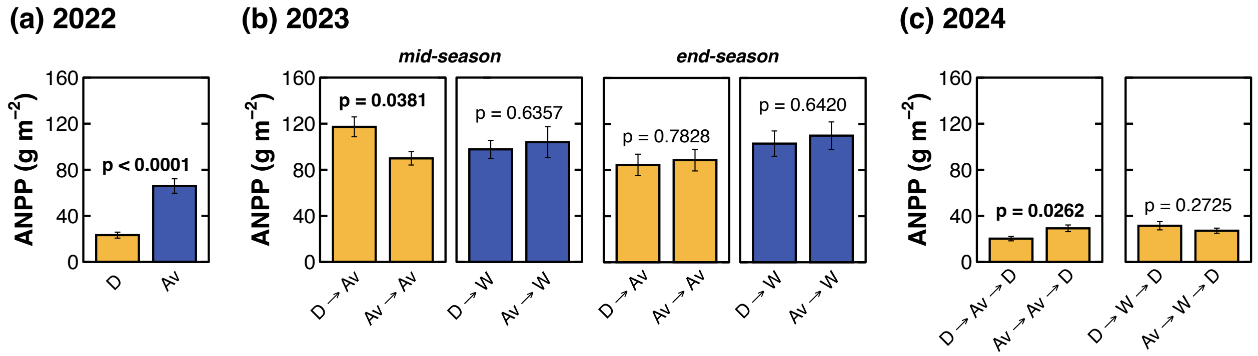
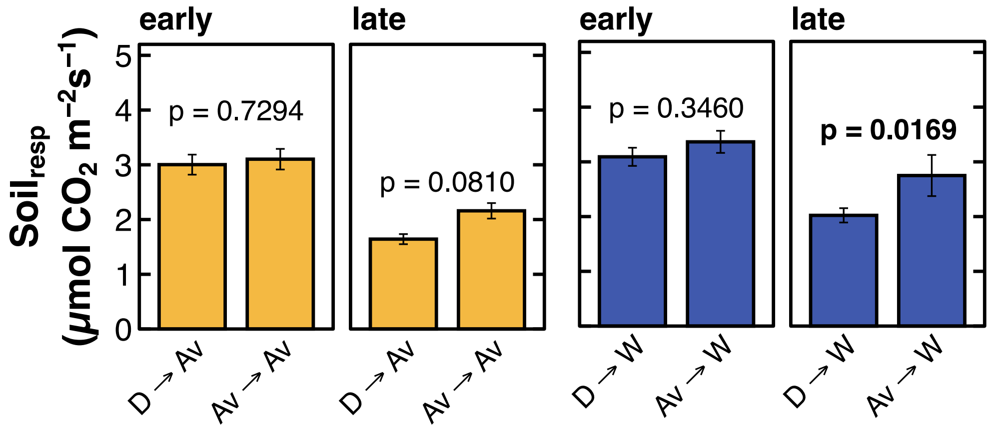


Figure 4.4. Aboveground net primary production (ANPP) at mid (2023 only) and end of season (all years) biomass harvests (mean ± 1 SE). Labels on x-axes correspond to conditions each year (D = extreme drought, Av = average, and W = extreme wet) and colors correspond to current conditions (wetter or drier each year). Precipitation manipulations were imposed from 2022–2023 by adding water, and legacy effects quantified both within the 2023 treatments (ambient average or experimental extreme wet) and from the previous two years during the 2024 natural extreme drought.

(a) 2023 Soil Respiration



(b) 2023 Nitrate (NO_3-N) Availability

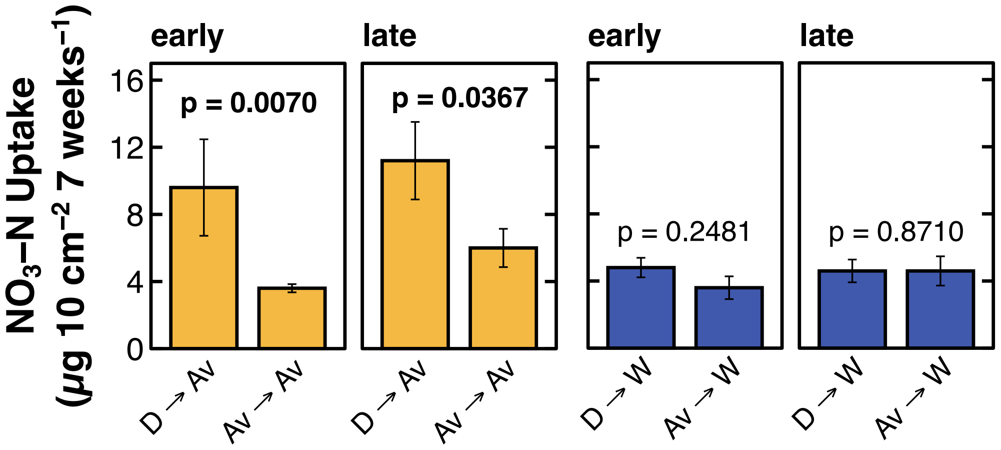


Figure 4.5. (a) Soil$_{Resp}$ and (b) NO3-N availability for 2023, averages (mean ± 1 SE) across each of the growing season periods – early-to-mid (prior to July 6) and mid-to-late (after July 6). Labels on x-axes correspond to conditions each year (D = extreme drought, Av = average, and W = extreme wet) and colors correspond to current conditions (wetter or drier each year). We quantified legacy effects within the 2023 treatments (ambient average – orange bars or experimental extreme wet – blue bars).

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CHAPTER 5: CONCLUSIONS

It is increasingly urgent to understand the impacts of precipitation extremes as they are increasing in frequency and magnitude with climate change (Trenberth et al. 2003, 2014; Ault 2020; Chiang et al. 2021; Chen et al. 2022; Vicente-Serrano et al. 2022; Tan et al. 2023; Zhu et al. 2024; Swain et al. 2025). Grassland and dryland productivity and ecosystems services are sensitive to changes in precipitation regimes, and, thus expected to respond strongly to future climate change (Noy-Meir 1973; Sala et al. 1988, 1992; Stuart-Haëntjens et al. 2018; Hoover et al. 2021; Smith et al. 2024). The ecosystem services provided by grasslands are numerous, but arid and semi-arid grasslands especially are often considered degraded or undesirable ecosystems (Rosen 2022; Bengtsson et al. 2019), even though they contribute significantly to global C-fluxes and provide forage for both domestic and natural grazers (Milchunas et al. 1988; O'Mara 2012; Poulter et al. 2014; Ahlström et al. 2015). The impacts of precipitation extremes on grassland structure and functioning are not limited to the period of the extreme, rather, impacts of extremes may persist after an extreme has subsided as "legacy effects" (Sala et al. 2012; Dudney et al. 2017; De Boeck et al. 2018; He et al. 2025).

There is growing evidence of the importance of precipitation legacy effects – the changes to ecosystem structure and functioning driven by antecedent precipitation extremes that persist post-extreme (Oesterheld et al. 2001; Sala et al. 2012; Dudney et al. 2017; Vilonen et al. 2022; Goodman and Felton 2025). Although our understanding of legacy effects is growing, most of the emphasis has been on legacy effects of drought, with fewer studies addressing legacy effects of increased precipitation, even though both extreme dry and wet years are expected under future climate scenarios (Tabari 2020; Gulev et al. 2021; Seneviratne et al. 2021; Douville et al. 2021). In my dissertation, I have explored ecosystem responses to both increased and decreased precipitation, from subtle differences within a single growing season to multi-year opposing extremes.

5.1 Research Summary

The results of my research demonstrate the variability in ecosystem responses to precipitation extremes and recovery dynamics after extremes end, especially showing the sensitivity of the shortgrass steppe to subtle differences in precipitation and other environmental variables. Experimental manipulations of drought have often been used to estimate ecosystem responses to the changes in drought frequency and timing due to climate change (Knapp et al. 2024). My first research chapter (Chapter 2) built on the knowledge gained from the Extreme Drought in Grassland Experiment (EDGE; Carroll et al. 2021). The EDGE project used identical methods to implement experimental drought treatments at four grasslands across the Central US. For my analysis, I used the existing EDGE data (4 years of experimental drought) combined with new data for the four years of recovery post-drought at each grassland and two additional pre-treatment years that included responses to the 2012 pan-continental drought. This decade-long dataset allowed me to update estimates of aboveground net primary productivity (ANPP) responses and grassland sensitivity to drought (Griffin-Nolan et al. 2018, 2019; Knapp et al. 2015) and compare recovery dynamics post-drought between the different types of droughts (natural vs. experimental) and grasslands.

First, my results provide further evidence for strong ANPP–PPT relationships across grassland types. The slope of my regression of the mean annual precipitation (MAP) and ANPP across the four sites was identical to the slope previously reported by Sala et al. (1988). Surprisingly, despite similar or greater reductions in precipitation due to the experimental drought compared to the natural drought, the natural drought caused greater reductions in ANPP (g m^{-2}) and greater sensitivity (ANPP g m^{-2} reduction per mm rainfall reduction) for all of the grasslands. Higher temperatures and greater vapor pressure deficit (VPD) likely contributed to the more negative responses of grasslands to the natural drought, and these results also add to growing evidence that drought experiments underestimate drought responses (Smith et al. 2024; Kröel-Dulay et al. 2022). Recovery dynamics varied between grasslands considerably and were not consistent for either of the drought types. There was evidence for both positive and negative drought legacy effects, but these differed by site and even within sites between natural and experimental drought. In my other two Chapters, I focused on responses to precipitation manipulations in just one of these four sites – the shortgrass steppe of northern Colorado.

In my first field project (Chapter 3), my goal was to manipulate spring precipitation to evaluate how different spring histories may affect the shortgrass steppe's response to a deluge within a single growing season. Originally, the intention was to reduce spring precipitation to levels that would simulate drought. However, soil moisture levels were only slightly reduced – remaining above-average for most of the spring (Saxton and Rawls 2006; Post and Knapp 2021; Hoover et al. 2022) despite using rain-out shelters that have been proven effective in previous studies (Gherardi and Sala 2013, Loik et al. 2019, Post and Knapp 2020). Although differences in soil moisture were much smaller and for a shorter period than originally intended, there were difference in deluge responses driven by legacy effects of the different spring conditions. Generally, responses to the deluge after the wetter spring were increased compared to responses from the drier spring. This was evident short-term for soil respiration, which increased significantly for the post-deluge response period only, and longer-term for canopy greenness (through the end of the growing season) and ANPP (regrowth from mid to late season and end of season total). As expected, the deluge addition did show compensatory effects for the drier spring – with similar responses between ambient conditions (without the deluge addition) and the drier spring + deluge treatment.

My second field experiment (Chapter 4) contributes to the growing interest in "hydroclimate whiplash" (Chen et al. 2022; Tan et al. 2023; Zhu et al. 2024; Mullens and Engström 2025; Swain et al. 2025) by evaluating the sensitivity of the shortgrass steppe to shifts between extreme drought, average, and extreme wet years. During the extreme natural drought of 2022, I used regular water addition treatments to simulate an average productivity response year. In 2023, I assigned those same plots to either the natural average year or to a watering treatment to simulate extreme wet growing season conditions. The study was extended for an additional year of observation as the 2024 growing season also was a natural extreme drought. Oesterheld et al. (2001) suggest that fluctuations in ANPP in semi-arid grasslands will be buffered during dry years if the preceding year was wet (a positive legacy effect) or will be amplified over multiple wet (growing greater) or dry (growing lower) years. Our results instead suggest that legacy effects of a preceding dry or wet year may be weak or irrelevant if the current year is also extreme, even if preceding year extremes were more severe. Most legacy effects of past years were limited to only a portion of the growing season if found at all. Under both extreme wet conditions in 2023 and extreme drought in 2024, the current year conditions dominated most ecosystem responses by the end of the growing season.

5.2 Implications and Future Directions

Overall, the results of my dissertation provide support for the strong effects of current extremes on grassland structure and functioning and identify examples of both positive and negative legacy effects following extremes. It is difficult to draw any overarching conclusions regarding legacy effects of precipitation extremes in grasslands due to the considerable variability in responses across grassland and drought types (Chapter 2), and at different time scales within the same grassland (Chapters 3-4). Instead, I would conclude that my results presented here show the high sensitivity of grasslands, and particularly the shortgrass steppe, to even subtle differences in environmental conditions. The results from Chapter 3 highlight the influence of subtle differences in soil moisture early in the season on responses to a deluge later. In Chapter 4, the watering treatments in 2022 and 2023 resulted in similar total growing season precipitation, but ecosystem functioning was quite different – most likely due to the increased temperatures, light, and vapor pressure deficit that would occur concurrently with the drought in 2022 and be reduced with the wetter conditions (especially in June) in 2023. These same environmental variables likely contributed to the differences between responses to 1-year natural and 4-year experimental drought in Chapter 2. The legacy effects identified in Chapters 3-4 were limited mostly to only portions of the growing season, but the effects on greenness and ANPP are relevant for management decisions. Mainly, the amount (e.g., ANPP) and timing (e.g. greenness) of forage availability (for livestock or native grazers) may differ from what is expected based on current and forecast conditions alone. With continued studies of legacy effects in specific grasslands more consistent patterns may be identified that would be more easily applicable to managers, especially following or during long-term consecutive extremes.

My results are somewhat limited by the confounding underlying extremes occurring naturally during field manipulations, but nonetheless can provide useful insights, especially for shorter-term legacy effects. Future studies would benefit from more careful control to avoid ambient extremes (such as implementing drought shelters for all treatments across an entire study period and adding all water rather than supplementing from ambient rainfall), or longer-term studies that would capture a better mix of extreme and average years. However, such controlled or long-term experiments are costly and consecutive extremes (in opposite or similar directions) may be more realistic under future climate scenarios than extremes followed by average years (Seneviratne et al. 2021; Tan et al. 2023). As the shortgrass steppe is already experiencing increased hydrological extremes – and is projected to continue to be subjected to such extremes into the future – this remains an important area of research and should be explored further, especially with an emphasis on temporal scales of extremes and legacy effects, and further investigation of the mechanisms driving such responses.

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APPENDIX 1

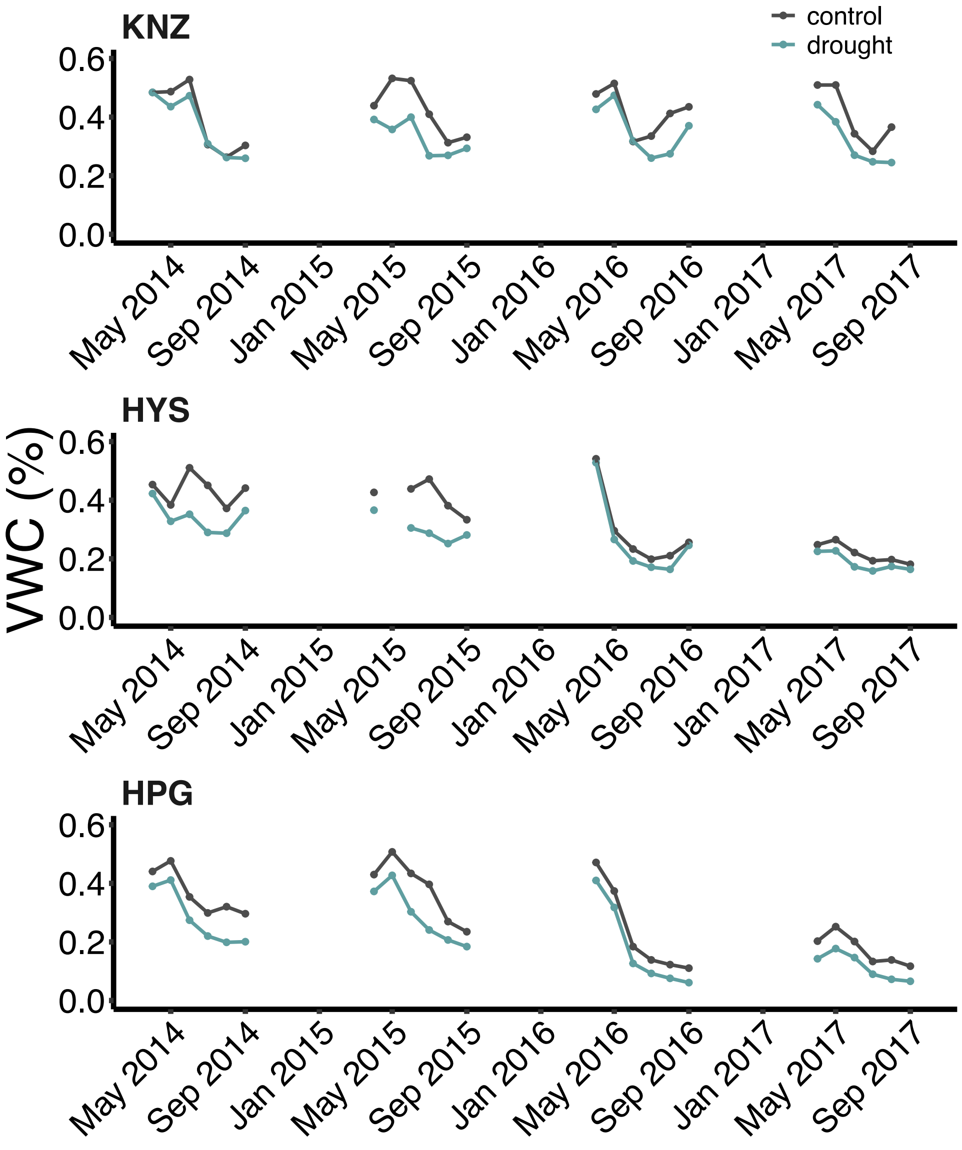


Figure A1.1. Monthly soil moisture volumetric water content (VWC, %) averages at three of sites (KNZ, HYS, and HPG) from April to September 2014-2017, each year of the experimental drought. Colors correspond to treatments (gray = ambient conditions, blue = droughted plots). Sensor issues prevent the inclusion of SGS. Figure adapted from Carroll et al. 2021.

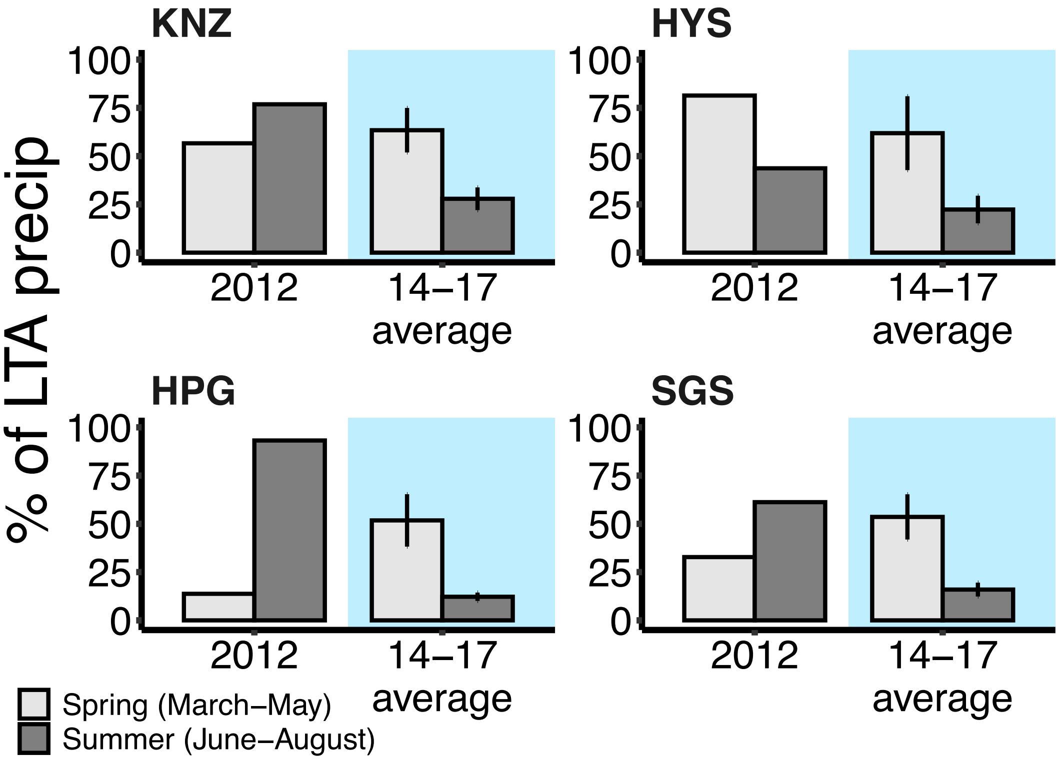


Figure A1.2. Seasonal patterns of precipitation in 2012 (natural drought) and 2014-2017 averaged (experimental drought) years. The 2012 natural drought reduced spring precipitation more than summer precipitation at all sites except for Hays while the 2014-2017 experimental drought years had the greatest precipitation reductions in summer.

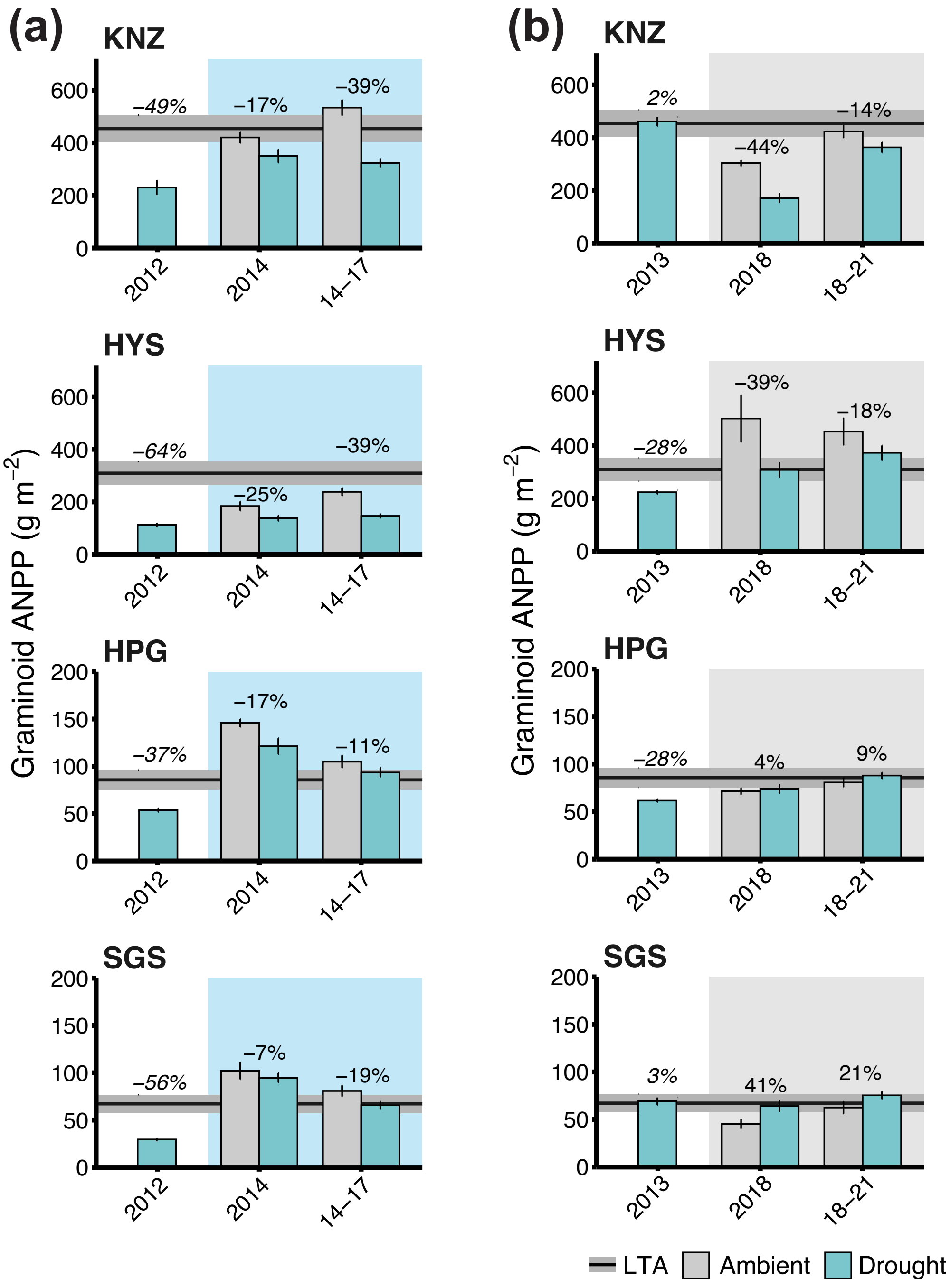


Figure A1.3. (a) Natural vs. experimental drought responses of graminoid species only. **(b)** Natural vs. experimental drought recovery of graminoid species. Both figures show natural drought (white background shading) compared to the 10-year graminoid average ANPP (horizontal bar and ±1 SE shading) for our experimental drought plots (light blue or gray background shading) to ambient plots during the drought experiment and recovery years.

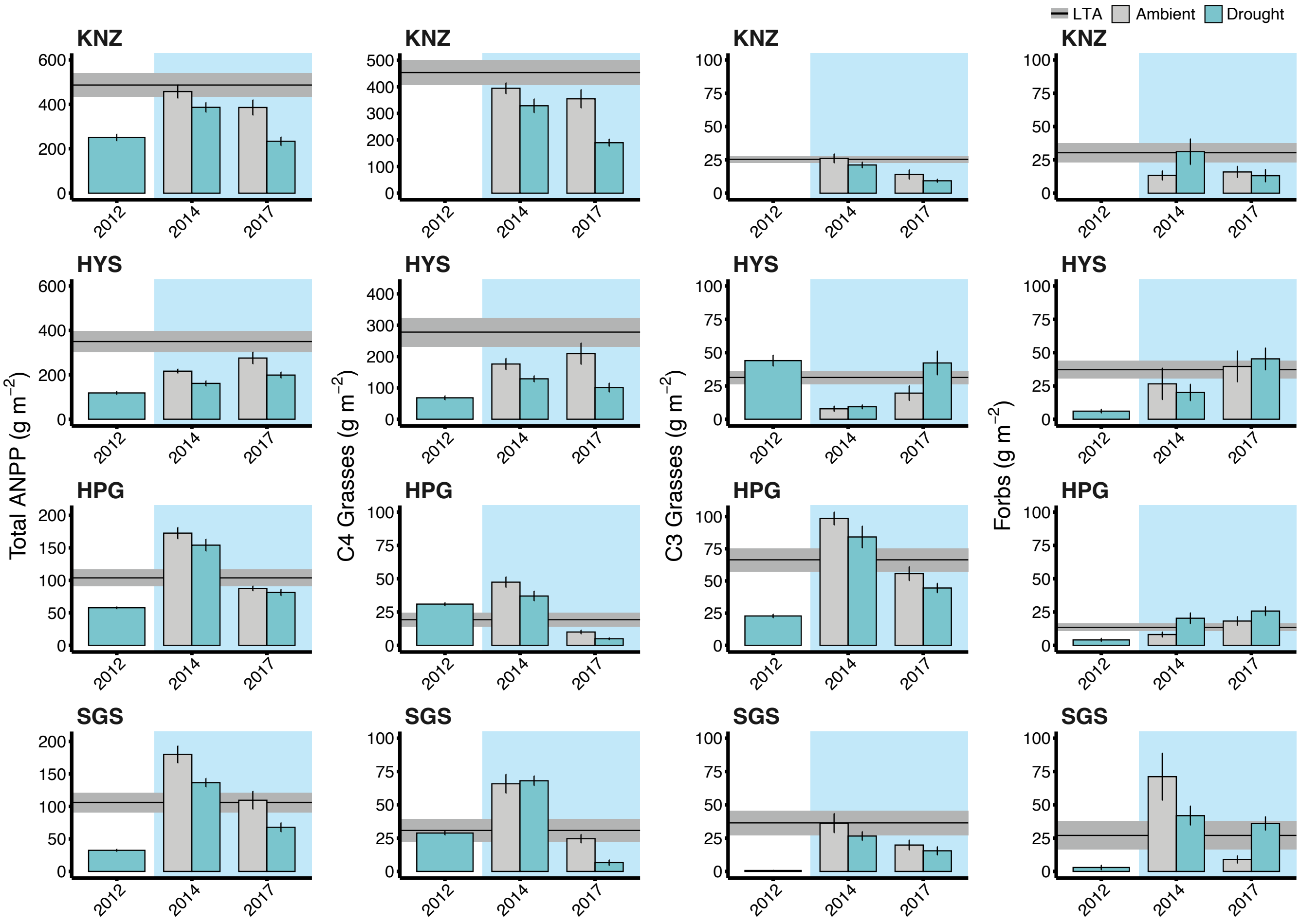


Figure A1.4. Responses in aboveground biomass for each function group (g m^{-2}) during the 2012 natural drought and the first and last years of experimental drought (2014 and 2017). Bars show average biomass for each year (± 1 SE) with gray bars for control plots and blue for droughted plots. Horizontal lines represent each site's 10-year average ANPP for each functional group (±1 SE shading), though averages at KNZ are based on 2013-2021 only as 2012 data was not divided into each functional group (hence also the exclusion of 2012 bars at KNZ).

Table A1.1. ANPP-PPT regression results for each site (Figure 1).

Model: ANPP ~ Annual Precipitation						
		Estimate	SE	t value	P-value	Model Adj. R^2
ALL	Intercept	-36.56	23.62	-1.548	0.126	0.724
	Precipitation	0.602	0.044	13.683	**<2e-16**	
KNZ	Intercept	93.44	95.01	0.983	0.340	0.447
	Precipitation	0.475	0.124	3.841	**0.001**	
HYS	Intercept	59.05	75.67	0.78	0.447	0.447
	Precipitation	0.473	0.123	3.838	**0.001**	
HPG	**Intercept**	112.31	26.5	4.238	**0.001**	-0.062
	Precipitation	-0.006	0.082	-0.072	0.944	
SGS	Intercept	48.514	27.93	1.737	0.102	0.166
	Precipitation	0.206	0.099	2.089	*0.053*	

Table A1.2. Ambient yearly precipitation and 30-year mean annual precipitation (MAP) for each site (mm). Annual precipitation is listed first, followed by growing season precipitation in parentheses. White background indicates values for natural drought/recovery year (2012-2013) and 30-year MAP, blue background for the experimental drought period (2014-2017), and gray background for the experimental recovery period (2018-2021). Within each period (natural, experimental drought, and experimental recovery), the driest annual and growing season precipitation years are bolded and the wettest italicized.

Year	KNZ	HYS	HPG	SGS
2012	**568.90** **(402.80)**	**366.00** **(249.90)**	**259.00** **(173.60)**	**217.50** **(137.50)**
2013	*783.40* *(574.80)*	*548.00* *(393.70)*	*462.90* *(333.80)*	*357.80* *(274.00)*
2014	**635.57** (476.04)	**458.68** (390.10)	333.00 (223.02)	293.24 (220.36)
2015	*1002.50* (725.80)	513.34 **(375.16)**	*355.09* *(282.96)*	*368.55* *(289.05)*
2016	945.14 *(763.50)*	*739.94* *(652.79)*	**256.79** **(211.33)**	**204.22** **(152.91)**
2017	720.20 **(447.00)**	570.49 (411.49)	281.43 (215.90)	288.54 (221.23)
2018	811.20 (504.90)	954.00 (657.10)	396.20 *(298.90)*	267.00 (182.70)
2019	*1131.10* *(865.70)*	786.30 (577.20)	*458.50* (297.60)	356.10 (230.50)
2020	807.90 (564.50)	**562.30** **(451.70)**	**255.40** **(165.70)**	**249.30** **(168.00)**
2021	**632.20** **(420.50)**	673.20 (485.50)	361.80 (215.90)	*397.98* *(286.28)*
MAP	856.46 (591.12)	614.68 (440.08)	385.13 (275.85)	334.34 (243.78)

Table A1.3. Yearly average daily mean temperatures and 30-year mean annual temperature (MAT) for each site (ºC). Annual temperatures are listed first, followed by growing season temperatures in parentheses. White background indicates values for natural drought/recovery year (2012-2013) and 30-year MAT, blue background for the experimental drought period (2014-2017), and gray background for the experimental recovery period (2018-2021). Within each period (natural, experimental drought, and experimental recovery), the hottest annual and growing season years are bolded and the coolest italicized.

Year	KNZ	HYS	HPG	SGS
2012	**14.37** **(22.88)**	**14.24** **(23.03)**	**9.02** **(16.51)**	**9.80** **(17.71)**
2013	*11.53* *(20.17)*	*12.14* *(20.88)*	*7.03* *(14.61)*	*7.96* *(15.80)*
2014	*11.85* (20.89)	*12.01* *(20.68)*	*7.30* *(13.85)*	*7.97* *(15.00)*
2015	13.48 (21.46)	**13.59** **(21.54)**	8.25 (14.42)	8.97 (15.51)
2016	**14.28** **(21.95)**	13.55 (21.08)	8.32 (14.55)	8.97 (15.56)
2017	13.76 *(20.88)*	13.25 (20.80)	**8.39** **(14.89)**	**9.08** **(15.92)**
2018	12.70 **(21.94)**	12.10 **(21.05)**	7.78 **(15.22)**	8.14 (15.93)
2019	*11.88* (20.66)	*11.49* (20.43)	*6.89* *(14.24)*	*7.27* *(15.20)*
2020	12.69 *(20.37)*	12.51 *(20.23)*	**8.16** (15.04)	8.74 (16.00)
2021	**13.36** (20.99)	**12.83** (20.83)	8.08 (14.79)	**8.98** **(16.25)**
MAT	12.50 (21.0)	12.40 (20.9)	7.59 (14.5)	8.29 (15.7)

Table A1.4. Yearly average mean daily VPD and 30-year VPD long-term averages (LTA) for each site (kPa). Annual values are listed first, followed by growing season in parentheses. White background indicates values for natural drought/recovery year (2012-2013) and 30-year LTA, blue background for the experimental drought period (2014-2017), and gray background for the experimental recovery period (2018-2021). Within each period (natural, experimental drought, and experimental recovery), the highest annual and growing season years are bolded and the lowest italicized.

Year	KNZ	HYS	HPG	SGS
2012	**1.10** **(1.67)**	**1.32** **(2.04)**	**1.00** **(1.51)**	**1.12** **(1.69)**
2013	*0.77* *(1.11)*	*1.02* *(1.55)*	*0.77* *(1.18)*	*0.87* *(1.32)*
2014	*0.83* **(1.21)**	1.03 **(1.50)**	*0.75* *(1.01)*	*0.85* *(1.16)*
2015	0.83 *(1.09)*	**1.06** (1.46)	0.79 (1.07)	0.90 (1.22)
2016	**0.86** (1.15)	*1.03* *(1.34)*	**0.85** (1.17)	**0.98** (1.34)
2017	0.85 (1.13)	1.04 (1.43)	0.84 **(1.20)**	0.95 **(1.35)**
2018	0.84 **(1.30)**	0.92 (1.35)	0.80 (1.18)	0.92 (1.37)
2019	*0.70* *(1.01)*	*0.84* *(1.24)*	*0.76* *(1.09)*	*0.85* *(1.26)*
2020	0.78 (1.05)	0.94 (1.29)	**0.95** **(1.39)**	**1.06** **(1.57)**
2021	**0.87** (1.16)	**0.99** **(1.35)**	0.85 (1.20)	0.98 (1.40)
VPD LTA	0.81 (1.16)	1.00 (1.45)	0.79 (1.14)	0.89 (1.30)

Table A1.5. Analyses and results for climate variables (Figure 2).

***One Sample T-test** comparing the percent of LTA precipitation during the 2012 natural drought compared to the average across the 2014-2017 experimental drought (n = 5 observations per site – one for each year). All experimental droughts showed a greater reduction from the LTA precipitation than the natural drought, though only HPG and SGS were significantly lower (or more severe).*

	% of LTA precipitation					95% CI	
Site	2012	2014-2017	t	df	p-value	Lower	Upper
KNZ	66.395	53.952	-1.845	3	0.1622	32.49	75.41
HYS	59.543	50.118	-1.036	3	0.3765	21.15	79.08
HPG	67.249	38.241	-6.517	3	**0.0073**	24.08	52.41
SGS	64.911	41.577	-4.022	3	**0.0276**	23.11	60.03

***ANOVA** for growing season average daily mean temperatures across sites for the natural (2012) and experimental 2014-2017 drought periods (n = 20 observations, 5 per site for each year). Across all sites, mean daily temperatures for 2012 were significantly higher than during the experimental drought. Model adjusted R^2 = 0.9851.*

Model: Temperature ~ Site + Natural vs. Experimental

	Sum sq	DF	F value	P-value
Intercept	1344.63	1	8338.548	**<0.0001**
Site	190.92	3	394.654	**<0.0001**
Natural vs. Experimental	12.46	1	77.289	**<0.0001**
Residuals	2.42	15		

***ANOVA** for growing season average daily mean VPD across sites for the natural (2012) and experimental (2014-2017) drought periods (n = 20 observations, 5 per site for each year). Across all sites, VPD was significantly higher in 2012 than during the experimental period. Model adjusted R^2 = 0.9066.*

Model: VPD ~ Site + Natural vs. Experimental

	Sum sq	DF	F value	P-value
Intercept	6.7118	1	1101.754	**<0.0001**
Site	0.3819	3	20.898	**<0.0001**
Natural vs. Experimental	0.7655	1	125.658	**<0.0001**
Residuals	0.0914	15		

Table A1.6. Repeated measures mixed effects ANOVAs for ANPP responses (g m^{-2}) over the entire 10-year study (Figure 3a). Responses are split by period: the natural drought (2012) and recovery (2013) years, experimental drought (2014-2017) years, and experimental drought recovery (2018-2021) years.

ANPP (g m^{-2}) responses during the 2012 natural drought vs. 2013 natural recovery year (n = 215 observations across all sites and both years). In 2012, the EDGE plots were not completed yet at KNZ, so measures come from n = 5 nearby plots. Since these plots are nearby, we include KNZ in the repeated measures ANOVA but results do not change whether KNZ is excluded or not. See Table S7 for responses of each year compared to LTAs. Model adjusted R^2 = 0.8984.

Model: log(ANPP) ~ Site * Year + (1|Plot)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	72.819	24.2732	3	116.86	290.55	**<0.0001**
Year	16.243	16.2433	1	140.09	194.549	**<0.0001**
Year*Site	6.888	2.2961	3	116.53	27.485	**<0.0001**

contrast	estimate	SE	df	t ratio	P-value
KNZ 2012-2013	-0.666	0.141	182.9	-4.727	**<0.0001**
HYS 2012-2013	-0.729	0.0774	99.5	-9.429	**<0.0001**
HPG 2012-2013	-0.166	0.0753	93.7	-2.2025	**0.0299**
SGS 2012-2013	-1.128	0.0753	93.7	-14.99	**<0.0001**

ANPP (g m^{-2}) responses during the experimental drought period. Model adjusted R^2 = 0.8478.

Model: log(ANPP) ~ Site*Year*Treatment + (1|Plot)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	77.62	25.8735	3	112.88	384.7125	**<0.0001**
Year	11.035	3.6784	3	330.77	54.694	**<0.0001**
Treatment	6.661	6.6609	1	112.99	99.0411	**<0.0001**
Site*Year	13.008	1.4454	9	330.56	21.4912	**<0.0001**
Site*Treatment	1.833	0.611	3	112.88	9.0856	**<0.0001**
Year*Treatment	0.802	0.2673	3	330.77	3.9742	**0.0084**
Site*Year*Treatment	1.526	0.1695	9	330.56	2.521	**0.0083**

	contrast	estimate	SE	df	t ratio	P-value
KNZ	2014 control-drought	0.18018	0.108	418	1.675	0.0948
	2015 control-drought	0.61402	0.108	418	5.707	**<.0001**
	2016 control-drought	0.54976	0.108	418	5.11	**<.0001**
	2017 control-drought	0.52791	0.108	418	4.907	**<.0001**
HYS	**2014 control-drought**	0.33398	0.116	426	2.88	**0.0042**
	2015 control-drought	0.64834	0.111	421	5.819	**<.0001**
	2016 control-drought	0.45547	0.112	423	4.057	**0.0001**

	2017 control-drought	0.34606	0.111	421	3.106	**0.002**
HPG	2014 control-drought	0.136	0.108	418	1.278	0.2069
	2015 control-drought	0.01743	0.108	418	0.162	0.8714
	2016 control-drought	-0.0567	0.111	422	-0.531	0.5958
	2017 control-drought	0.10124	0.108	418	0.941	0.3473
SGS	**2014 control-drought**	0.27194	0.109	419	2.506	**0.0126**
	2015 control-drought	0.4747	0.108	418	4.412	**<.0001**
	2016 control-drought	0.00472	0.109	419	0.044	0.9653
	2017 control-drought	0.49754	0.109	419	4.586	**<.0001**

ANPP (g m^{-2}) recovery following the experimental drought period (2018-2021). Model adjusted R^2 = 8772.

Model: log(ANPP) ~ Site*Year*Treatment + (1|Plot)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	123.956	41.319	3	112.07	452.1119	**<0.0001**
Year	14.952	4.984	3	331.24	54.5346	**<0.0001**
Treatment	0.006	0.006	1	112.08	0.0695	0.79257
Site*Year	20.8111	2.312	9	331.2	25.3014	**<0.0001**
Site*Treatment	0.974	0.325	3	112.07	3.5519	**0.01675**
Year*Treatment	0.607	0.202	3	331.24	2.2122	0.08653
Site*Year*Treatment	1.852	0.206	9	331.2	2.2518	**0.01869**

	contrast	estimate	SE	df	t ratio	P-value
KNZ	**2018 control-drought**	0.4293	0.13	399	3.304	**0.001**
	2019 control-drought	0.203	0.134	407	1.511	0.1316
	2020 control-drought	-0.0297	0.134	407	-0.221	0.8254
	2021 control-drought	-0.0125	0.13	399	-0.096	0.9233
HYS	**2018 control-drought**	0.2591	0.131	401	1.977	**0.0487**
	2019 control-drought	-0.1607	0.13	399	-1.237	0.2169
	2020 control-drought	-0.056	0.131	401	-0.427	0.6694
	2021 control-drought	0.3309	130	401	2.525	**0.012**
HPG	2018 control-drought	-0.0823	0.13	399	-0.634	0.5268
	2019 control-drought	-0.0782	0.13	399	-0.602	0.5474
	2020 control-drought	-0.331	0.131	401	-2.527	**0.0119**
	2021 control-drought	-0.1671	0.134	407	-1.243	0.2144
SGS	2018 control-drought	-0.2406	0.13	399	-1.851	0.0648
	2019 control-drought	-0.096	0.13	399	-0.739	0.4604
	2020 control-drought	-0.0555	0.13	399	-0.427	0.6696
	2021 control-drought	-0.0849	0.13	399	-0.654	0.5137

Table A1.7. Results of repeated measures ANOVA for natural drought ANPP (g m^{-2}) responses in 2012 (Figure 3b) and recovery in 2013 (Figure 5) compared to all other years.

ANOVA *of ANPP responses to the 2012 natural drought compared to 2013-2021 ambient ANPP (n = approx. 560 ambient plots across all sites and 10-yrs). All sites showed significant reductions in ANPP during the 2012 natural* drought. *Model adjusted* R^2 *= 0.7989.*

Model: log(ANPP) ~ Site * Period + (1|Plot/Period)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	106.284	35.428	3	203.09	207.412	**<0.0001**
Period	32.707	32.707	1	307.29	191.609	**<0.0001**
Site * Period	6.145	2.048	3	203.09	11.992	**<0.0001**

contrast	estimate	SE	df	t ratio	P-value
KNZ 2012 vs. 9-yrs	-0.666	0.1910	455	-3.487	**0.0005**
HYS 2012 vs. 9-yrs	-1.023	0.0873	151	-11.718	**<0.0001**
HPG 2012 vs. 9-yrs	-0.493	0.0857	148	-5.757	**<0.0001**
SGS 2012 vs. 9-yrs	-1.173	0.0856	147	-13.710	**<0.0001**

ANOVA *of ANPP responses during the 2013 recovery year from natural drought compared to 2012-2021 ambient ANPP (not including 2013; n = approx. 560 ambient plots across all sites and 10-yrs). KNZ and HYS showed no significant difference in ANPP in 2013 compared to their LTAs, but significant differences or potential legacies were evident at SGS and HPG. Model adjusted* R^2 *= 0.6723.*

Model: log(ANPP) ~ Site * Period + (1|Plot/Period)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	166.451	55.484	3	128.70	209.7271	**<0.0001**
Period	0.200	0.200	1	128.92	0.7546	0.3866
Site * Period	3.391	1.130	3	182.70	4.2728	**0.0065**

contrast	estimate	SE	df	t ratio	P-value
KNZ 2013 vs. 9-yrs	0.0572	0.125	118	0.456	0.6490
HYS 2013 vs. 9-yrs	0.0035	0.124	135	0.028	0.9778
HPG 2013 vs. 9-yrs	-0.2251	0.120	131	-1.875	0.0631
SGS 2013 vs. 9-yrs	0.3769	0.120	130	3.143	**0.0021**

Table A1.8. Results of repeated measures mixed effects ANOVAs to compare ANPP responses (g m^{-2} mm^{-1}) during natural (2012) and experimental (2014-2017) drought periods.

*ANPP sensitivity response (g m^{-2} mm^{-1}) in the <u>first year</u> of natural (2012) and experimental (2014) droughts. The Site*Year interaction effect was not significant, so the model was run again dropping that variable and with a cube root transformation of the response variable to meet model assumptions. Across all sites, the responses to natural and experimental drought were significantly different. Model adjusted $R^2 = 0.5175$.*

Model: $ANPP^{1/3}$ ~ Site + Natural vs. Experimental + (1|Block)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	0.4744	0.1581	3	32.855	7.7014	**0.0005**
Natural vs. Experimental	1.0089	1.0089	1	34.945	49.1447	**<0.0001**

*ANPP sensitivity response (g m^{-2} mm^{-1}) to the natural drought (2012) compared to the <u>average across experimental drought years</u> (2014-2017). The Site*Year interaction effect was not significant, so the model was run again dropping that variable and with a log transformation of the response variable to meet model assumptions. Across all sites, the responses to natural and experimental drought were significantly different.*

Model: ANPP ~ Site + Natural vs. Experimental + (1|Block/Natural vs. Experimental)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	6.6774	2.2258	3	35.935	23.435	**<0.0001**
Natural vs. Experimental	6.4753	6.4753	1	64.704	68.200	**<0.0001**

Table A1.9. Simple linear regression ANOVAs for ANPP responses (g m^{-2}) during the first recovery year following experimental drought (2018) and averaged across the entire experimental drought recovery period (2018-2021; Figure 5).

ANOVA of ANPP responses during the 2018 recovery year from experimental drought in ambient and experimentally/simulated droughted plots. Significant differences of pairwise comparisons indicate legacy effects of the experimental drought at those sites.

Model: log(ANPP) ~ Site * Treatment

	Sum sq	df	F value	P-value
Intercept	199.168	1	2315.428	**<0.0001**
Site	31.626	3	122.555	**<0.0001**
Treatment	0.045	1	0.5253	0.4701
Site*Treatment	1.901	3	7.3685	**0.0002**
Residuals	9.548	111		

contrast	estimate	SE	df	t ratio	P-value
KNZ control vs. drought	0.4293	0.114	111	3.780	**0.0003**
HYS control vs. drought	0.2679	0.115	111	2.338	**0.0212**
HPG control vs. drought	-0.0823	0.114	111	-0.725	0.4701
SGS control vs. drought	-0.2406	0.114	111	-2.118	**0.0364**

Repeated measures ANOVA of ANPP responses over the entire 2019-2021 recovery period following experimental drought in ambient and experimentally/simulated drought plots.

Model: log(ANPP) ~ Site * Treatment + (1|Plot)

	Sum sq	Mean sq	NumDF	DenDF	F value	P-value
Site	236.633	78.878	3	112.01	389.336	**<0.0001**
Treatment	0.024	0.024	1	112.04	0.1172	0.7327
Site * Treatment	1.864	0.621	3	112.01	3.0674	**0.0309**

contrast	estimate	SE	df	t ratio	P-value
KNZ control vs. drought	0.1366	0.0887	115	1.540	0.1264
HYS control vs. drought	0.0962	0.0877	111	1.097	0.2752
HPG control vs. drought	-0.1737	0.0881	113	-1.972	0.0511
SGS control vs. drought	-0.1193	0.0872	109	-1.368	0.1740

APPENDIX 2

Table A2.1. Number of observations and outliers included for each analysis. Total observations = all useable data collected, and outliers were identified and significant outliers (based on Bonferroni p-values) removed before analysis.

	number of observations		
Response Variable	**total**	**outliers**	**analysis**
Soil$_{VWC}$ 0-20 cm	1208	4	1204
Soil$_{VWC}$ 0-50 cm	1536	0	1536
GCC	906	8	898
Soil$_{resp}$	400	3	397
End of Season ANPP	40	1	39
Mid to Late ANPP	40	1	39
NO3 Availability	40	1	39

Table A2.2. Results of linear mixed effect model ANOVAs for each continuously measured response variable (0-20 cm Soil$_{VWC}$, GCC, and Soil$_{resp}$) associated with line graphs over the growing season. Identical analyses were run for each response variable on the full data (including all three treatments over the entire growing season) and on data with ambient treatments combined for all dates before the experimental deluge addition (as shown in line graphs).

Full Treatments

Soil Moisture (Soil$_{VWC}$)	***df***	***F***	***p***
Treatment	2, 37.57	8.0957	**0.0012**
Date	33, 1065.65	189.7034	**< 0.0001**
Treatment × Date	66, 1065.64	19.0127	**< 0.0001**

Canopy Greenness (GCC)	***df***	***F***	***p***
Treatment	2, 37.14	13.6271	**< 0.0001**
Date	23, 789.65	129.6458	**< 0.0001**
Treatment × Date	46, 789.59	9.6601	**< 0.0001**

Soil Respiration (Soil$_{resp}$)	***df***	***F***	***p***
Treatment	2, 16.99	6.2739	**0.0091**
Date	19, 320.05	83.533	**< 0.0001**
Treatment × Date	38, 320.05	4.1	**< 0.0001**

Combined Early Ambient Treatments

Soil Moisture (Soil$_{VWC}$)	***df***	***F***	***p***
Treatment	2, 94.59	32.717	**< 0.0001**
Date	33, 1085.10	171.212	**< 0.0001**
Treatment × Date	66, 1084.82	26.257	**< 0.0001**

Canopy Greenness (GCC)	***df***	***F***	***p***
Treatment	2, 91.59	82.5017	**< 0.0001**
Date	23, 800.49	110.8563	**< 0.0001**
Treatment × Date	35, 800.17	7.8797	**< 0.0001**

Soil Respiration (Soil$_{resp}$)	***df***	***F***	***p***
Treatment	2, 38.74	18.141	**< 0.0001**
Date	19, 328.72	84.072	**< 0.0001**
Treatment × Date	29, 328.51	4.224	**< 0.0001**

Table A2.3. Results of linear mixed effect model ANOVAs for each continuously measured response variable (0-20 cm and 0-50 cm Soil_{VWC}, GCC, and $\text{Soil}_{\text{resp}}$) associated with bar graphs averaged over each deluge response period. Identical analyses were run for each response variable on the full data (including all three treatments over the entire growing season) and on data with ambient treatments combined for all dates before the experimental deluge addition (as shown in bar graphs).

Full Treatments

0-20 cm Soil Moisture (Soil_{VWC})	***df***	***F***	***p***
Treatment	2, 38.42	12.132	**< 0.0001**
Deluge Period	3, 1157.22	446.273	**< 0.0001**
Treatment × Deluge Period	6, 1157.21	47.393	**< 0.0001**

0-50 cm Soil Moisture (Soil_{VWC})	***df***	***F***	***p***
Treatment	2, 9.09	7.6254	**0.0114**
Deluge Period	3, 1515.00	2190.7349	**< 0.0001**
Treatment × Deluge Period	6, 1515.00	24.9683	**< 0.0001**

Canopy Greenness (GCC)	***df***	***F***	***p***
Treatment	2, 41.40	20.86	**< 0.0001**
Deluge Period	3, 852.12	191.481	**< 0.0001**
Treatment × Deluge Period	6, 851.99	16.055	**< 0.0001**

Soil Respiration ($\text{Soil}_{\text{resp}}$)	***df***	***F***	***p***
Treatment	2, 18.12	2.1094	0.1501
Deluge Period	3, 368.07	117.0663	**< 0.0001**
Treatment × Deluge Period	6, 368.07	5.9827	**< 0.0001**

Combined Early Ambient Treatments

0-20 cm Soil Moisture (Soil_{VWC})	***df***	***F***	***p***
Treatment	2, 91.20	16.332	**< 0.0001**
Deluge Period	3, 1167.4	419.068	**< 0.0001**
Treatment × Deluge Period	4, 1164.9	66.476	**< 0.0001**

0-50 cm Soil Moisture (Soil_{VWC})	***df***	***F***	***p***
Treatment	2, 25.61	28.413	**< 0.0001**
Deluge Period	3, 1518.29	1934.921	**< 0.0001**
Treatment × Deluge Period	4, 1517.78	24.369	**< 0.0001**

Canopy Greenness (GCC)	*df*	*F*	*p*
Treatment	2, 87.20	46.785	**< 0.0001**
Deluge Period	3, 863.95	182.747	**< 0.0001**
Treatment × Deluge Period	4, 862.01	11.993	**< 0.0001**

Soil Respiration (Soil$_{resp}$)	*df*	*F*	*p*
Treatment	2, 36.66	8.6149	**0.0009**
Deluge Period	3, 374.52	123.2278	**< 0.0001**
Treatment × Deluge Period	4, 373.32	5.0675	**0.0005**

Table A2.4. Results of simple linear regressions and ANOVAs for (1) end of season ANPP and (2) mid to late season ANPP (regrowth).

End of Season ANPP	***df***	***F***	***p***
Intercept	1	176.7878	**< 0.0001**
Treatment	2	4.9682	**0.0124**
Residuals	36		

Mid to Late ANPP	***df***	***F***	***p***
Intercept	1	100.271	**< 0.0001**
Treatment	2	14.735	**< 0.0001**
Residuals	36		

Table A2.5. Results of simple linear regression and ANOVA for NO_3-N availability over 60 days (from directly before the experimental deluge addition to ~ 2 months after).

Nitrate-N	***df***	***F***	***p***
Intercept	1	588.554	**< 0.0001**
Treatment	2	11.964	**0.0001**
Residuals	36		

APPENDIX 3

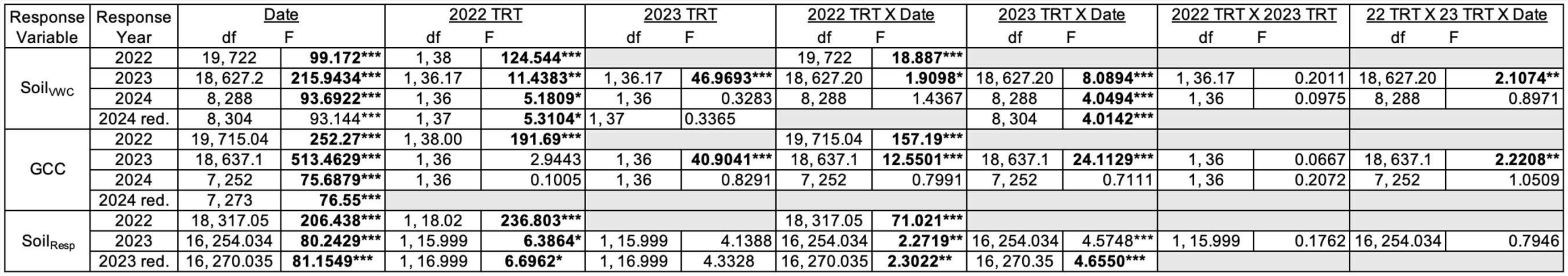
Table A3.1. Continuous responses across growing season. t or F values with "*", "**", and "***" are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

Response Variable	Response Year	2022 TRT		2023 TRT		2022 TRT X 2023 TRT	
		df	t or F	df	F	df	F
Soil_{VWC}	2022 (t)	31.453	-10.26***				
	2023	1, 36	3.834	1, 36	20.5227***	1, 36	0.2547
	2023 red.	1, 37	10.938**	1, 37	48.749***		
	2024	1, 36	1.7262	1, 36	0.0090	1, 36	0.1377
	2024 red.	1, 38	5.1882*				
GCC	2022 (t)	20.666	-14.073***				
	2023	1, 36	1.5007	1, 36	23.0261***	1, 36	0.0815
	2023 red.	1, 37	4.1758*	1, 37	43.3341***		
	2024	1, 36	0.2982	1, 36	0.9327	1, 36	0.2072
	2024 red.						
$\text{Soil}_{\text{Resp}}$	2022 (t)	12.641	-12.897***				
	2023	1, 16	1.6789	1, 16	0.9689	1, 16	0.2782
	2023 red.	1, 17	5.8159*	1, 17	3.8478		

Table A3.2. Continuous responses across growing season periods. F values with "*", "**", and "***" are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

Response Variable	Response Year	Period		2022 TRT		2023 TRT		2022 TRT X Period		2023 TRT X Period		2022 TRT X 2023 TRT		22 TRT X 23 TRT X Period	
		df	F	df	F	df	F	df	F	df	F	df	F	df	F
Soil$_{VWC}$	2022	1, 38	0.2969	1, 38	111.5290***			1, 38	5.5085*						
	2023	1, 36	1481.869***	1, 36	10.5613**	1, 36	45.6230***	1, 36	0.8171	1, 36	30.8186***	1, 36	0.1963	1, 36	2.5202
	2023 red.	1, 39	823.779***	1, 37	10.796**	1, 37	46.636***								
	2024	1, 36	2.5107	1, 36	5.2699*	1, 36	0.3442	1, 36	1.0404	1, 36	1.7347	1, 36	0.0965	1, 36	0.9890
	2024 red.			1, 38	5.4954*										
GCC	2022	1, 38	182.90***	1, 38	190.30***			1, 38	115.62***						
	2023	1, 36	219.8217***	1, 36	3.0881	1, 36	45.2054***	1, 36	56.9941***	1, 36	96.4364***	1, 36	0.0757	1, 36	6.1133*
	2024	1, 36	8.3929**	1, 36	0.1001	1, 36	0.7697	1, 36	0.0083	1, 36	0.2418	1, 36	0.1036	1, 36	1.2242
	2024 red.	1, 39	8.7346**												
Soil$_{Resp}$	2022	1, 18	267.099***	1, 18	170.970***			1, 18	11.251**						
	2023	1, 16	97.3644***	1, 16	5.3927*	1, 16	3.6133	1, 16	4.6495*	1, 16	2.3536	1, 16	0.3038	1, 16	0.0081
	2023 red.	1, 19	80.3920***	1, 18	4.8737*										

Table A3.3. Continuous responses across growing season dates. F values with "*", "**", and "***" are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively



Response Variable	Response Year	Date		2022 TRT		2023 TRT		2022 TRT X Date		2023 TRT X Date		2022 TRT X 2023 TRT		22 TRT X 23 TRT X Date	
		df	F	df	F	df	F	df	F	df	F	df	F	df	F
Soil$_{\mathrm{VWC}}$	2022	19, 722	**99.172*****	1, 38	**124.544*****			19, 722	**18.887*****						
	2023	18, 627.2	**215.9434*****	1, 36.17	**11.4383****	1, 36.17	**46.9693*****	18, 627.20	**1.9098***	18, 627.20	**8.0894*****	1, 36.17	0.2011	18, 627.20	**2.1074****
	2024	8, 288	**93.6922*****	1, 36	**5.1809***	1, 36	0.3283	8, 288	1.4367	8, 288	**4.0494*****	1, 36	0.0975	8, 288	0.8971
	2024 red.	8, 304	93.144***	1, 37	**5.3104***	1, 37	0.3365			8, 304	**4.0142*****				
GCC	2022	19, 715.04	**252.27*****	1, 38.00	**191.69*****			19, 715.04	**157.19*****						
	2023	18, 637.1	**513.4629*****	1, 36	2.9443	1, 36	**40.9041*****	18, 637.1	**12.5501*****	18, 637.1	**24.1129*****	1, 36	0.0667	18, 637.1	**2.2208****
	2024	7, 252	**75.6879*****	1, 36	0.1005	1, 36	0.8291	7, 252	0.7991	7, 252	0.7111	1, 36	0.2072	7, 252	1.0509
	2024 red.	7, 273	**76.55*****												
Soil$_{\mathrm{Resp}}$	2022	18, 317.05	**206.438*****	1, 18.02	**236.803*****			18, 317.05	**71.021*****						
	2023	16, 254.034	**80.2429*****	1, 15.999	**6.3864***	1, 15.999	4.1388	16, 254.034	**2.2719****	16, 254.034	4.5748***	1, 15.999	0.1762	16, 254.034	0.7946
	2023 red.	16, 270.035	**81.1549*****	1, 16.999	**6.6962***	1, 16.999	4.3328	16, 270.035	**2.3022****	16, 270.35	**4.6550*****				

Table A3.4. Aboveground net primary production (ANPP) model results for full and reduced (if needed) models at each collection point. t or F values with "*", "**", and "***" are significant at p < 0.05, p < 0.01, and p < 0.001, respectively

Response Variable	Response Year	2022 TRT		2023 TRT		2022 TRT X 2023 TRT	
		df	t or F	df	F	df	F
End Season	2022 (t)	25.311	**-6.2982*** **				
	2023	1, 34	0.0772	1, 34	1.6417	1, 34	0.0183
	2023 red.			1, 36	3.767		
	2024	1, 36	**5.3797***	1, 36	**8.3945****	1, 36	**5.8954***
Mid Season	2023	1, 35	**4.6464***	1, 35	2.3658	1, 35	3.4074
End Growth	2023	1, 36	1.4263	1, 36	**4.5583***	1, 36	0.3841

Table A3.5. Soil N availability in 2023, averaged across the growing. F values with "*", "**", and "***" are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

Response Variable	Response Year	2022 TRT		2023 TRT		2022 TRT X 2023 TRT	
		df	F	df	F	df	F
NO_3-N	2023	1, 16	**6.7283***	1, 16	**6.3747***	1, 16	2.3079
	2023 red.	1, 17	6.2476*	1, 17	**5.9193***		

Table A3.6. Soil N availability in 2023, compared between the early-to-mid and mid-to-late growing season periods. F values with "*", "**", and "***" are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

Response Variable	Response Year	Period		2022 TRT		2023 TRT		2022 TRT X Period		2023 TRT X Period		2022 TRT X 2023 TRT		22 TRT X 23 TRT X Period	
		df	F	df	F	df	F	df	F	df	F	df	F	df	F
NO_3-N	2023	1, 16	**6.2297***	1, 16	**6.7283***	1, 16	**6.3747***	1, 16	1.7990	1, 16	2.2542	1, 16	2.3079	1, 16	0.0480
	2023 red.	1, 19	**5.8848***	1, 17	**6.2476***	1, 17	**5.9193***								

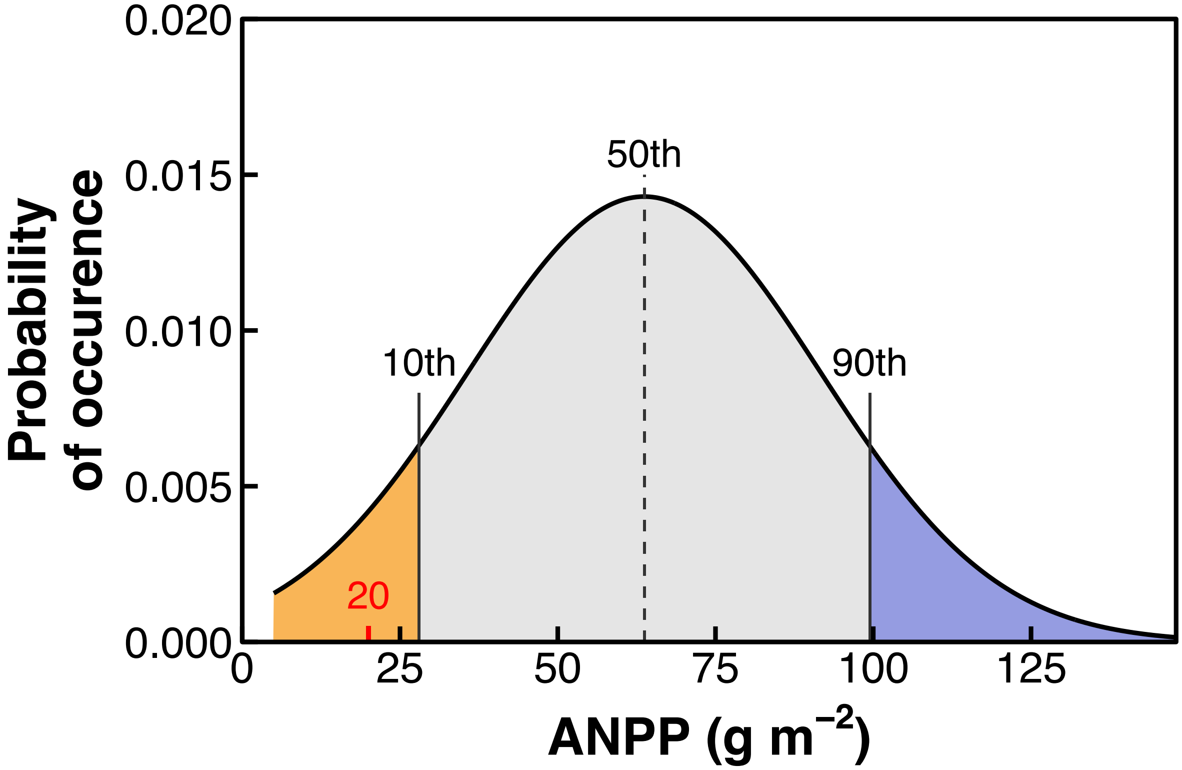


Figure A3.1. Normal distribution curve of estimated probability of occurrence of aboveground net primary productivity (ANPP) based on long-term ANPP records. We classified ambient conditions in 2022 and 2024 as extreme droughts since ANPP was ~20-23 g m-2 in those years (below the 10th percentile), and 2023 as an average year with ~80 g m-2 (between the 10th and 90th percentiles).

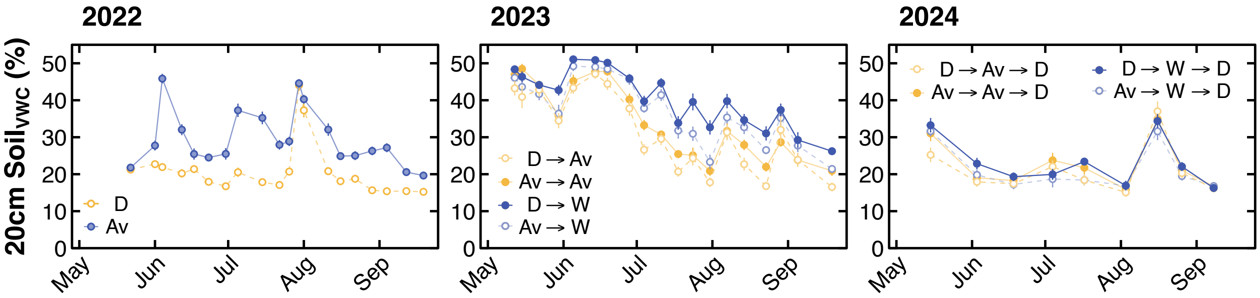


Figure A3.2. Daily measurements of Soil$_{VWC}$ (treatment mean ± 1 SE) over each growing season. Legend letters correspond to each year's combination of current and antecedent conditions: 2022 D (extreme drought) vs. Av (average); 2023 Av (average) vs. W (extreme wet); and 2024 D (extreme drought).

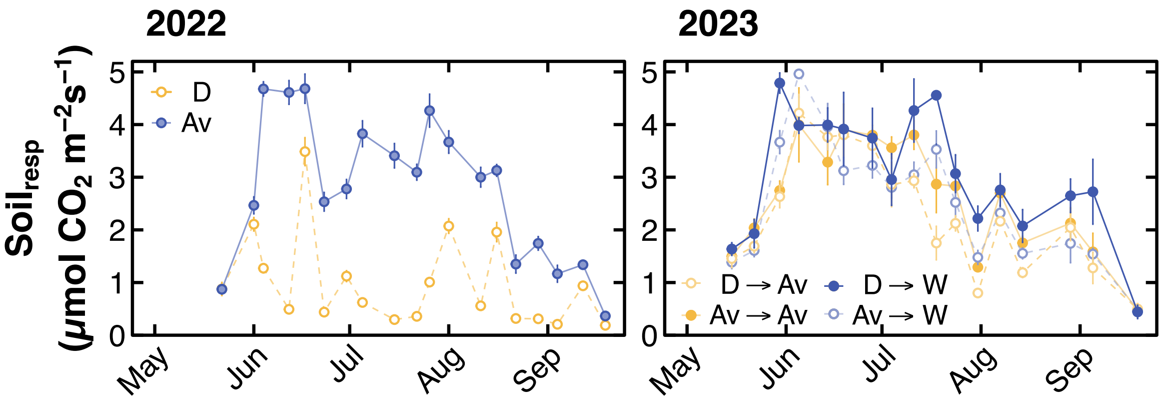


Figure A3.3. Daily measurements of Soil$_{Resp}$ (treatment mean ± 1 SE) during the 2022-2023 growing seasons. Legend letters correspond to each year's combination of current and antecedent conditions: 2022 D (extreme drought) vs. Av (average); and 2023 Av (average) vs. W (extreme wet). Soil$_{Resp}$ was not measured in 2024 but would be expected to remain low with little or no legacy effects from previous conditions under the extreme drought.